The male voice:
an evolutionary perspective

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ABSTRACT

The introduction to this thesis outlines the evolutionary theory of human mating behaviour and describes the process of vocal production and auditory perception in humans. In addition it provides a brief overview of some of the research studies examining the role of vocalisations in courtship and competitive behaviours in animals. The body of this thesis is then divided into three parts.

Part 1 examined whether male vocal frequencies may be an honest signal of physical attributes such as body size, body shape and hormonal quality. Results of Study 1 found that fundamental frequency but not formant dispersion was related to age. The voices of younger (but post-pubertal) males had lower fundamental frequency. Furthermore, fundamental frequency was significantly negatively associated with shoulder and chest circumferences, shoulder-hip-ratio and body weight. A significant negative relationship was also found between formant dispersion and both weight and height and some measures of body shape. Study 2a and 2b then found evidence of a relationship between fundamental frequency and circulating testosterone in adult males with some evidence for diurnal variation in fundamental frequency (reflecting alterations in testosterone). Some limited evidence of a relationship between formant dispersion and circulating testosterone was also found. No relationship between prenatal testosterone or cortisol and vocal frequencies was observed.

The second part of this thesis explored the role of the male voice in both inter and intra sexual selection. Study 3 examined perceptions of male voices by male listeners. Results revealed that the judgements made by male listeners concerning the age and physique of male speakers were broadly consistent with the relationships observed between physical characteristics and vocal frequencies in Study 1. Results also suggested that formant frequencies and not fundamental frequency indicate the dominance of a speaker but that both vocal parameters inform judgements that male listeners make about the attractiveness of male speakers to females. Study 4 examined perceptions of male voices by female listeners. Results suggest that both fundamental and formant frequencies influence judgements of attractiveness and dominance. In addition the relationship between visual and vocal attractiveness and dominance was examined. No relationship was observed between visual and vocal attractiveness although there was a significant relationship between visual and vocal dominance.

The final section of this thesis examined the relative importance of the voice in comparison to the face within the context of attraction and dominance. Results of two studies suggest that vocal and visual attractiveness and dominance may not be related and that the relative importance of facial and vocal cues depends upon the judgement being made. The face appears to have a greater influence on attractiveness judgements but the voice appears to have a greater influence on judgements of dominance.

The results of the studies reported in this thesis are discussed in relation to the findings of other researchers in the field which together provide evidence that the five criteria for sexual selection of communication signals (Snowden, 2004) are met by the deep voice of the human male. Furthermore, I speculate that the evolution of low fundamental frequencies and low formant

frequencies in the male voice may have evolved under separate selection pressures.

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PREFACE

A person's voice is known to convey a considerable amount of information about the speaker quite apart from what is being said. For example, listeners are known to make attributions and judgements about the age (Linville, 1996; Mulac & Giles, 1996), personality (Addington, 1968 and Aronovitch, 1976) and socioeconomic status (Ellis, 1967) of a speaker based on their voice. However, the most common inference made about a voice is the sex of the speaker and listeners are easily able to distinguish between an adult male and an adult female voice (Bennett & Montero-Diaz, 1982; Childers & Wu, 1991; Coleman, 1976). The ease with which the sex of a speaker can be identified is because an adult male voice is considerably deeper than that of an adult female or prepubescent child due to the changes in the larynx that occur during puberty. But why do these changes take place and what purpose does a deep voice in the human male serve? The central aim of this research programme is to address these questions from a functional perspective by proposing that a deep voice is a characteristic or trait that has evolved in the human male because it plays a role in human sexual attraction and competition within this context – namely, attracting female mates and intimidating male rivals.

In evolutionary terms, one the most fundamental challenges any individual faces, is to successfully select a mate in order to reproduce and pass on their genes to the next generation. Possibly the most complex and intriguing of all human behaviours is how we go about meeting this challenge. Charles Darwin (1871) proposed that some traits or characteristics may have evolved to enhance an individual's success at finding a mate. Darwin described this process or mechanism as 'sexual selection' - the evolution of a characteristic or trait because of its reproductive benefit. Such a characteristic may enhance mating success through two processes: by attracting opposite-sex mates (intersexual selection) and/or, by intimidating same-sex rivals (intrasexual selection). Such characteristics emerge at puberty, under the influence of the sex steroid hormones (principally testosterone), and are thought to influence the process of mate choice.

Returning to the voice, evidence suggests that non human primates and many other animals make mating decisions based on acoustic cues and that such cues are also an important factor in competitive behaviours (for a review see Kelley & Brenowitz, 2002). But is this the case in humans?

Tinbergen (1952) identified four perspectives which, when considered together, provide a theoretical and methodological framework for studying biological traits. Tinbergen suggested that such traits can only be completely explained by addressing questions of mechanism, ontogeny, function and phylogeny. Birdsong is an example of a trait that has been successfully studied within this framework (Konishi et al., 1989) so that our understanding of birdsong far exceeds many other areas of animal behaviour (Hauser, 1996). In order to completely explain a trait such as the deep voice of the human male we should explore proximate explanations; ie. understand the physiological mechanisms that produce a deep voice (physiological) and how it develops within the individual (ontogenetic) and also ultimate explanations;

ie. how it evolved (evolutionary) and what function a deep voice serves (functional).

Much is known about the mechanisms that produce a deep voice and the ontogeny of the male voice (reviewed in the introduction to this thesis). Questions about how a deep voice may have evolved in the human adult male may remain elusive since the soft tissues of the larynx do not fossilise, however, researchers, including myself, have now turned their attention to studies attempting to understand the function of this trait in order to provide a more comprehensive explanation for the existence of this sexually dimorphic trait. The central argument of this thesis is that a deep voice in the human male may be a sexually selected trait that has evolved in order to intimidate male rivals and/or attract female mates.

It is important to note that it is the voice as an acoustic signal that is being examined here and not language or speech *per se*. According to the *Source-Filter Theory of Speech Production* (Muller 1848; Fant 1960), the human voice consists of two independent acoustic components – fundamental frequency (the primary determinant of the perceived pitch of a vocalization) and formant (or resonant) frequencies. Fundamental frequency (F_o) is determined by the vibration of the vocal folds, and formant frequencies are determined by the size and shape of the vocal tract and by the movement of the articulators. At puberty in human males, changes in the larynx under the influence of the testosterone permanently lower fundamental frequency (Jenkins, 1998). A subsequent secondary descent of the larynx also produces lower formant frequencies and less formant dispersion (D_f) which simply means that the formants are closer together (Fitch & Giedd, 1999). The acoustic effect of both of these physical changes contributes to a deeper, more imposing voice in an adult male relative to a prepubescent child or adult female. A deep male voice is therefore a sexually dimorphic trait that emerges at sexual maturation and is dependent, in part at least, on sex hormones. It is thus a likely candidate for sexual selection.

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DECLARATION

I declare that the work contained in this thesis has not been submitted for any other award and that it is all my own work.

Name: Sarah Evans

Signature:

Date:

Chapter 1

INTRODUCTION

The central argument of this thesis is that the deep voice of human males may be an important factor in both human courtship and competitive behaviours. This introductory chapter first outlines the evolutionary theory of mating behaviours setting the theoretical context for the examination of the evolution of a deep voice in the human male as a sexually selected trait within this context. In support, examples are presented from the comparative literature providing evidence that acoustic signals are known to play a significant role in both courtship and competitive behaviours in many animal species. Finally, in order to examine the role of the human voice in this context, some knowledge about the physics of the voice is necessary. This chapter therefore outlines vocal production and the ontogeny of the voice in humans and finally briefly describes auditory perception of voices.

1.0 Evolutionary theory

Evolution refers to the gradual change in the inherited traits of an organic population over successive generations. In the early twentieth century Darwin's theory of natural selection, which sought to describe the mechanism of evolution, was combined with Mendel's discovery of the gene as a single unit of inheritance to provide a unifying explanation for the diversity of life on earth. Fundamental to Darwin's theory is the concept of selection, a process by which only organisms best adapted to their environment survive and transmit their genetic characteristics to succeeding generations.

1.1 Natural Selection

Natural selection, as described by Darwin in "On the Origin of Species" (1859), favours those traits that improve the probability of survival and reproduction. Individuals possessing such favourable traits are more likely to survive and reproduce so that, if the trait has variability and also has a heritable component, it becomes more prevalent in successive generations. In this case the trait is said to be 'selected for' whereas those traits that reduce success are said to be 'selected against' and become rarer. Over time, successive small changes may result in adaptations that specialise organisms for particular ecological niches and may even eventually give rise to the emergence of new species.

1.1.1 Types of selection

Selection can be categorised into three different types: directional, disruptive, and stabilizing. Directional selection is a shift in the mean value of a trait towards one extreme and away from the extreme selected against. Disruptive selection is selection for extreme values of the distribution of a trait within a population so that the average value is selected against and therefore becomes less common over time, producing a bi-modal distribution at the extremes. Finally, stabilizing selection is selection against extreme values such that mean values of a trait are maintained decreasing variation in the expression of the trait concerned (Trivers, 1985).

1.1.2 Fitness

Fitness is a central concept of natural selection. It refers to the reproductive outcome of an individual in terms of their ability to pass on their genes to subsequent generations. An individual's fitness is manifested through its phenotype. An individual's phenotype is the sum of its observable characteristics determined by both its genotype (its genetic make up) and the influence of the environment in which it lives. The fitness of individuals with the same genotype is not necessarily equal because of subtle environmental differences. Since the fitness of a genotype is an averaged quantity, the term fitness is generally used to reflect the reproductive outcomes of all individuals with a given genotype.

1.2 Sexual selection

Sexual selection is often referred to as a special case of natural selection although both may interact or overlap. It refers to the mechanism by which a trait or characteristic evolves because it enhances reproductive success even if it potentially lowers survival under the process of natural selection.

Sexual selection occurs more often in males than females and Darwin proposed that this process of sexual selection may account for some of the extreme differences observed between the sexes and the evolution of extravagant male ornaments such as the peacock's *(Pavo cristatus)* tail and the red deer stag's *(Cervus elaphus)* antlers. Both of these examples confer a reproductive benefit to the beholder that compensates for the lowered survival probability the trait confers under natural selection. In this sense, sexual selection has the ability to evolve 'maladaptive' traits. Darwin said "Sexual selection … depends, not on a struggle for existence, but on a struggle between males for possession of females; the result is not death to the unsuccessful competitor, but few or no offspring" (Darwin, 1859 p88).

There are several reasons why sexually selected traits occur more often in males than females including (but not limited to) variance in reproductive success, differential parental investment and the operational sex ratio:

1.2.1 Variance in reproductive success

In a classic study of fruit flies *(Drosophila melanogaster)* Bateman (1948) showed that reproductive success varied more amongst males than females. He observed that the fertility of the female fruit fly is limited by her ability to produce eggs, but the fertility of the male is limited by the number of females he inseminates. If a male mates with several females he increases his number of progeny but a female gains little from copulation with many males, having many mates does not increase a female's reproductive success and may in fact reduce it (Trivers, 1972 and Parker, 1979). Multiple mating has been shown to reduce reproductive success in females in at least 15 different species of insects (Arnquist & Nilsson, 2000) and exposure to compounds in male seminal fluid has been shown to reduce the survival and fecundity of females (eg. Brown et al. 2004). However, Priest, Galloway & Roach (2008) recently examined the effect of female multiple mating on both mothers and their daughters. In agreement with previous studies they found that mothers with high mating frequency had reduced survival (on average they had 50% shorter lives) and 30% lower reproductive success than mothers with low mating frequency. Their results also suggested that multiple mating accelerated the aging process. However, their novel results found that high maternal multiple mating improved the lifetime reproductive success and fitness of their daughters, improving total fecundity by 28%. Indeed, in terms of inclusive fitness there was no evidence that increased mating frequency had fitness costs; the direct cost of maternal multiple mating being balanced or traded off by the benefit to female offspring. These results suggest that multiple mating may not be as costly to females as previously assumed in this species at least. However, in species where the number of offspring produced by a female is relatively predictable or varies little whereas the number of offspring that may be produced by a male varies considerably, in humans for example, males may still be under strong selection pressure to mate with many females whereas selection pressures on the female may act to make her choosey about which male fathers her progeny. This pattern has been observed in many species (see Clutton-Brock, 1988 for a review). When there is high variance in male reproductive success and low variance in female reproductive success the mating system is usually polygamous and competition between males for access to females is high. Such variance in reproductive success may lead to the evolution of distinctive morphological and behavioural male traits to intimidate male rivals and to attract multiple female mates.

1.2.2. Differential Parental investment

Trivers' (1972) suggested that differential parental investment is a driving force behind the process of sexual selection. Sex differences in gamete size may constitute differential initial investment, with ova being larger and more costly in terms of energy than sperm, however, the term investment also includes the relative contributions of resource provision and care for offspring. For example, in many mammal species, sexual intercourse for females may lead to a long period of pregnancy and an extended period of lactation and parental care; whereas for males parental investment may be minimal, ending at fertilization. One prediction that follows from this theory is that because human females typically make a greater parental investment (ie. they are the higher investing sex), they are more selective about mating, and males (who are the lower investing sex) must compete for access to them by developing secondary sexual ornaments that leads to greater sexual dimorphism. In monogamous species where parental investment is similar little sexual dimorphism is observed and both sexes may discriminate among and compete over potential mates; whereas in species where paternal investment in offspring is high female competition is high (Clutton-Brock, 1991; Gwynne, 1991).

1.2.3 Operational sex ratio

The operational sex ratio (OSR) is defined as the ratio of males to females who are capable of reproduction at a given time (Andersson, 1994). It affects the intensity of same-sex competition for mates since the sex with the largest number of individuals capable of mating compete for access to the opposite sex. When there are equal numbers of males and females the intensity of competition is equal in males and females, however, when there are more males than females (ie. the sex ratio is skewed), competition between males is high and competition between females is low. In a population in which there are as many sexually mature males as females (a ratio of 1:1) any sex difference in the rate of reproduction will skew the OSR (Emlen & Oring, 1977). A male-biased sex ratio is thought to lead to stronger sexual selection of male traits (but see Arnqvist, 1992).

1.2.4. Sex role divergence model

Kokko & Jennions (2008) challenged Trivers' arguments that initial asymmetry between gametes (anisogamy) promotes divergence in continued parental investment and a male-biased OSR. Instead they present an integrative mathematical model that shows how several factors may interact and influence each other to generate divergent sex roles. These factors include: the care needs of offspring, sexual selection, multiple mating, the OSR and also the ASR (adult sex ratio).

1.3 Intrasexual and Intersexual selection

Sexual selection arises in response to either same-sex competition (usually between males), or choice by the opposite-sex (usually female choice) or, less commonly, a combination of both.

1.3.1 Intrasexual selection

Intrasexual selection, occurs when members of one sex (usually males) compete against one another for access to opposite sex mates. Sexual selection may favour those attributes or characteristics that enable an individual to win physical contests or simply intimidate rivals allowing the 'victor' greater access to potential mates. Examples of such sexually-selected traits are the canine teeth of male baboons and the antlers of red deer stags.

Competition between males for female mates is a key concept behind Darwin's theory of sexual selection. Competition in this context is referred to in the broadest sense. Not only does it include direct contests or fighting but also indirect or passive competition simply through mate choice by the other sex. Darwin proposed that mate choice itself initiates a struggle between individuals of the same sex "*to excite or charm the opposite sex*" (Darwin, 1871).

1.3.2 Intersexual selection

Intersexual selection occurs through mate choice; usually female choice. It is important to note when discussing sexual selection that the term "mate choice" is defined broadly and is not restricted to conscious or deliberate choice but refers to the behaviour patterns or preferences of the female that make them more likely to mate with some potential partners rather than others. Darwin himself said "*It would be more correct to speak of the females as being excited or attracted to a special degree by the appearance, voice etc. of certain males rather than deliberately selecting them*" (Darwin 1859). In their article "*Mate Choice Turns Cognitive*" Miller and Todd (1998) suggested a "computational theory" of mate choice in which sexual cues are perceived that provide reliable information about potential mates; these cues are then used to estimate underlying trait values such as health, fertility and social status; these estimates are then used to choose a mate.

1.4 Sexually selected traits

Sexually-selected morphological traits emerge at sexual maturity, timed to influence the process of mate choice, and are under the influence of the sex hormones (Cronin, 1991; Gould & Gould, 1989). An example of such a characteristic from the animal kingdom is the silver back of the adult male gorilla that advertises high social status, attracting females (intersexual selection) and intimidating male rivals (intrasexual selection) and also conferring to the bearer the advantage of such status through access to food and provisions (Schaller, 1963). Characteristics like this evolve because individuals possessing them are more successful in competition for mates with same sex rivals (intrasexual selection) and are chosen more often as mates by the opposite sex (intersexual selection) so that they are more successful at passing on their genes. There are three main hypotheses that seek to explain the existence of such features:

1.4.1 The good genes theories

a) Handicap principle

Zahavi (1975) proposed that females look for traits that are costly to produce or cause “handicap” to the individual such as fine antlers in deer stags. These secondary sexual ornaments reduce the probability of survival and therefore honestly display an individual’s ability to withstand the handicap the trait infers, advertising the quality of his genotype. Only “costly” handicaps are honest indicators since “cheap” signals would be easy for low quality imitators to fake (Zahavi & Zahavi, 1997).

b) ***Parasite resistance hypothesis***

This explanation is a modification of the handicap principle and suggests that epigamic traits (those traits that are most attractive to the opposite sex) are honest signals of low parasitic load (Hamilton & Zuk, 1982) so that they indicate an individual’s ability to withstand the ravages of parasitism and other disease-causing organisms. Only healthy, vigorous males will display “showy” secondary traits. Hamilton and Zuk’s (1992) study of North American passerine birds found that birds infected with blood parasites had less bright plumage and produced less complex bird song, both of these being ornaments preferred by females of the species.

c) Immunocompetence

Related to the handicap principle and an elaboration of parasitic resistance theory, but providing a mechanistic approach, Folstad and Karter (1992) proposed that testosterone, which influences the development of secondary characteristics at puberty, does so at a cost to the immune system. Their proposal (since referred to as the Immunocompetence Handicap Hypothesis) argued that testosterone has an immunosuppressive effect so that males have a greater susceptibility to infection including parasitism. Only males with superior immune systems will therefore be able to develop and maintain these androgen-dependent, enhanced secondary characteristics that honestly advertise their superior immunocompetence. Individuals with less efficient or defective immune systems may be able to display the characteristic but not maintain the same standard since viruses and other pathogens disrupt the physical development of such traits.

In support of their theory Folstad and Karter (1992) noted that a variety of secondary sexual characteristics (including vocalizations, agonistic behaviours, display behaviours, and visible morphological features) are related to testosterone in a dose-dependent manner. For example, in a review of immune function and sexual selection in birds, Møller et al., (1998) demonstrated that in species where male plumage is used by females as an assessment of mate quality, plumage brightness was associated with markers of immune defence, and the brightest males were consistently chosen by females as mates. Similarly, Saino et al., (1999) found that tail length and colouration reflected the immune status of male barn swallows. Møller and Petrie (2002) tested whether different sexual signals provide information about different aspects of phenotypic quality in male blue peafowls. In this species, train length demonstrated condition-dependent expression, but different aspects of this feature were associated with different measures of immunocompetence. Such findings are consistent with a ‘multiple messages hypothesis’ (see section 1.7.1) suggesting that different aspects of a multiple ornament may signal different aspects of quality (see Møller & Pomiankowski, 1993).

1.4.2 Runaway selection

Fisher (1930) proposed that some traits evolve simply because females prefer them and not because they indicate male quality or stimulate pre-existing sensory bias in the female sensory systems. If the trait has a heritable component then females who mate with males with attractive traits will produce “sexy sons”, and daughters who will have similar sexual preferences to their mothers. The increasing prevalence of the preference exerting pressure for the trait to become more and more extreme (runaway selection) until the benefits in terms of mating success are checked by natural selection (Kodric-Brown & Brown, 1985) or all genetic variation is lost. Although the model does not explain how a stronger preference leads to the exaggeration of the trait it is thought that runaway selection may be a powerful evolutionary force (Maynard-Smith, 1985, Kirkpatrick, 1982).

1.4.3 **Sensory bias (exploitation)**

This theory suggests that sexually selected traits may have nothing to do with good genes or male quality. Such signals may simply be more conspicuous and easy to recognise because they exploit pre-existing biases in the female sensory system. They have therefore evolved due to selection upon males to be noticed by females.

The mechanisms described above may work alone or in combination in the evolution of sexually selected traits so that they cannot be considered as mutually exclusive.

1.5 The null hypothesis

Barber (1995) suggests that traits have not been influenced by sexual selection if the following criteria are violated:

a) The trait is sexually dimorphic
b) The trait is not directly involved in reproduction
c) The trait is most pronounced at age of breeding
d) The trait is either attractive to mates or intimidating to rivals
e) The trait influences reproductive success
f) The trait exhibits variability across the life course and between individuals of the same sex
g) The trait's expression is dependent on sex hormones.

1.6 Examples of morphological traits in human males that are candidates for sexual selection

1.6.1 Beards

One example of a sexually selected morphological trait in human males is facial hair. Beards are sexually dimorphic, emerge at puberty under the influence of testosterone and do not appear to have any obvious survival value (Barber, 1995). Beards may have played a role in attracting female mates and intimidating male rivals in our evolutionary past before it was possible to manipulate beard hair growth through shaving. In a study using pictures in which the fullness of beards had been manipulated, physical attractiveness ratings increased as the amount of beard hair increased (Hatfield & Sprecher, 1986). Another study (Pellegrini, 1973) using photographs of the faces of real males who shaved their beards in stages found that both male and female judges rated photographs of fuller beards as better-looking, and also rated them higher on a number of sociosexual dimensions including dominance and masculinity. In addition they rated the photographs of subjects with fuller beards as being older. Barber (1995) suggested that beards may be an example of runaway selection. Other studies (eg. Feinman & Gill,1977) however report negative associations between beards and personality attributes and it may be that facial hair is more associated with intimidation than with attraction.

1.6.2 Male body build

Body build is also sexually dimorphic with males having a larger upper body musculature, biceps and broader shoulders (Ross & Ward, 1982). These features are created at puberty via the action of testosterone on muscle mass. A number of studies using silhouettes as stimuli have shown that women prefer males with well developed physiques but not extreme muscular physiques suggesting that runaway directional selection has not occurred (Barber, 1995). Height is another sexually dimorphic trait with tall (although, again, not extremely tall) men enjoying more dating success (Jackson, 1992; Shepperd & Stathman, 1989) and shown to have higher reproductive success than short men (Mueller & Mazur, 2001; Pawlowski et al., 2000). Barber (1995) suggests that since extreme height and extreme body build are not preferred that they are not a ‘good genes’ sexually selected trait but rather that they are cues to resource quality. There is evidence to suggest that aspects of body build may be assortative preferences; the female preference being relative to the female's own body build, for example, assortative preferences for physical traits such as height (Pawlowski, 2003) and weight (Allison et al, 1996) have been shown. Again, these features provide mixed cues – an attractive component to females and an intimidation component to males.

1.6.3 Male faces

Averageness and facial symmetry are preferred in male faces and it is argued by Thornhill and Gangestad (1993) that both advertise parasitic resistance. However, there are many examples of deviations from average that are also found attractive such as large chin size, large cheekbones and large square jaws (eg. Cunningham, 1986; Cunningham et al., 1990). Thornhill and Gangestad (1993) propose that since enlarged facial features in men are produced by pubertal bone growth, for which testosterone is thought to be responsible, such characteristics therefore advertise superior immunocompetence. Generally, Barber (1995) proposes that since facial attractiveness is reliably correlated with various indicators of fitness, the evolution of some such traits can be explained in terms of the ‘good genes’ model of sexual selection. There is some evidence from studies using 'morphed' facial photographs that women's preferences for male faces vary across the menstrual cycle with more masculine faces being preferred at ovulation, and more feminine faces being preferred at other phases of the menstrual cycle (Penton-Voak et al., 1999). These researchers suggest that women seek a trade-off between mates with good genes at ovulation when they are likely to conceive and good fathers with feminised features indicating nurturing ability and potential parental investment at other times.

1.6.4 Bilateral symmetry

Fluctuating asymmetry (FA), representing deviations from bilateral symmetry for a number of morphological traits, is thought to be an important indicator of genetic quality and phenotypic fitness in both sexes (Thornhill & Gangestad, 1999), with low fluctuating asymmetry reflecting an individual's ability to withstand genetic and environmental stresses. Low FA has been shown to be associated with increased genetic, physical and mental health (Thornhill & Møller, 1997).

1.6.5 Male voices

The human voice is sexually dimorphic with adult males having a considerably deeper voice than adult females or prepubescent children of either sex. Although Darwin was the first to suggest that a deep voice may be a sexually selected trait, it was not until recently that attention has returned to the examination of a deep voice as a sexually-selected trait. At the start of this research programme only one paper had been published that had examined female preferences for male voices (Collins, 2000). In this study stimuli consisted of the voices of 34 males aged between 18 and 34 years of age reciting the English vowel sounds. Fifty four female judges between the ages of 18 and 30 rated the attractiveness of the stimuli. Voices with low fundamental frequency and low formant frequencies (both of which combine to produce a deep voice) were rated as the most attractive. Collins proposed that a deep voice may have evolved in the human male under selection pressure from male-male competition and/or through selection pressure due to women's preference for deeper voices. As the male voice is the topic of this thesis, past and current research in this area will be reported in detail later.

1.7 The use of multiple cues

Several examples of male morphological traits in humans that are thought to have evolved through sexual selection have been briefly reviewed. The question of whether these independent traits or indeed separate features of particular traits, operate as single signals providing information about different aspects of quality or whether they provide back-up signals of the same qualities is a much under researched area. In the main, each trait has been investigated separately without consideration to any interaction between them. However, sexual displays designed to attract opposite-sex partners are often very complex involving many different components or cues that may occur across different sensory modalities. For example, many male bird species possess bright ornamentation and also perform elaborate song. Whilst the use of such multiple cues in mate choice was recognised by Darwin (1871) it was not until recently that increased attention was paid to the possibility that mate choice may be based on several cues and not just one decisive signal. Different hypotheses have been proposed that seek to explain why females may use multiple cues and not just one (see Candolin, 2003 for a full review).

1.7.1 Multiple messages hypothesis

According to the multiple messages hypothesis (Møller & Pomiankowski, 1993; Johnstone, 1997), different signals give different information about different mate qualities. Each signal either provides a cue of a different aspect of quality that once evaluated together give a clearer indication of overall quality, or the receiver may pay attention to different aspects of mate quality depending on their own condition or genetic make-up (Wedekind, 1992) or indeed varying social and physical conditions (Reid & Weatherhead, 1990; Kodric-Brown, 1993; Endler & Houde, 1995; Marchetti, 1998).

1.7.2 The back-up (or redundant) signal hypothesis

Whereas the multiple messages hypothesis suggests that each signal reflects a different aspect of quality, according to the back-up signal hypothesis (Møller & Pomiankowski, 1993) each signal reflects the same quality but with some error. Paying attention to multiple signals therefore allows a more accurate assessment of quality, reducing errors and the time and energy inspecting mates and possibly the ability for potential mates to cheat about their quality. Since few studies have reported positive correlations between male traits it is suggested that back-up signals are less common than multiple messages (Candolin, 2003).

1.7.3 Fisherian cues

Holland & Rice (1998) suggest that many multiple signals may not reflect quality but are generally Fisherian cues that occur alongside viability indicators improving signal detection and/or reception or that they are remnants from past selection and are maintained as thresholds for maintaining female interest.

1.7.4 Receiver psychology

This hypothesis suggests that signallers may use signals with multicomponents to elicit a greater response from the receiver than a single component by enhancing the detection (eg. reducing reaction time, increasing the probability of detection or lowering detection threshold), recognition, discrimination or memorability of the signal. Rowe (1999) suggests that receiver psychology may play an important role in signal evolution.

1.7.5 Multiple sensory environments

This hypothesis suggests that different signals may be used under different environmental conditions, for example, some traits may increase detection at a distance whereas others reflect quality at closer range, with the cue most easily assessed being used depending upon the condition.

1.7.6 Multiple receiver hypothesis

Often neglected in recent literature, the multiple receiver hypothesis suggests that different signals may coexist because they are directed at different receivers (Butcher & Rohwer, 1988; Andersson, 1994 and Savalli, 1995). For example, the red-collared widowbird (*Euplectes ardens*) possesses at least two ornaments – a long tail and red carotenoid plumage and Pryke et al. (2001) proposed that female choice is based primarily on tail length whist the red carotenoid coloration functions primarily as a signal in competitive encounters between males.

1.7.7 Interaction of multiple cues

Multiple cues may be used in an additive way (Kunzler & Bakker, 2001) or the interaction between them may be more complex, for example, the attention females pay to one cue may be dependant on the expression of another or one cue may influence the cost or expression of another. Interaction between cues is thought to be common in the animal kingdom although most research in human research continues to focus on the examination of individual traits. One study (Grammer et al., 2001) investigated multiple signals in relation to female attractiveness. Participants judged the attractiveness of female stimuli in three poses (face, front nude with face covered, and back nude). They found a significant correlation between the ratings of each pose and propose that, in line with the back-up signal hypothesis, women's faces and bodies therefore form a single ornament that indicates honest mate value since features of the face, back and front are all related to oestrogen. No similar research has yet been undertaken in men. Fink and Penton-Voak (2002) point out that research that is limited to individual features may be inherently limited if attractiveness cannot be reduced to the analysis of a single feature.

1.8 Personal and behavioural attributes

As previously reviewed, multiple morphological traits such as male body build, facial hair, symmetry etc. may be used by human females to assess the physical quality of potential male mates. Evolutionary speaking human females should prefer a partner with secondary sexual characteristics that advertise good genes. However, there are other personal and behavioural traits that are also thought to influence female mate preferences.

In most mammals sexual relationships are brief, however, many male humans invest heavily in parenting (Geary, 2000; Geary & Flinn, 2001) which extends the potential length of human relationships so that they may range from very brief sexual encounters to long-term partnerships including marriage. However, the costs of reproduction are higher for human females than males since their rate of reproduction is much slower so that females are predicted to be the choosey sex in both short and long term contexts.

Human females are predicted to prefer long term, dominant partners who are able to provide protection and are willing to invest resources in both the female and their offspring. There is considerable cross-cultural evidence to suggest that females value good financial prospects (Buss, 1989) and high social status (Buss & Schmitt, 1993) in a potential marriage partner. They also prefer dominant males (Sadella et al, 1987) who are likely to confer greater access to resources. Further, the ability and willingness to engage in parenting activities is an important preference (La Cerra, 1994). Personal and behavioural characteristics like these provide information about the willingness of a male to make a long term investment in the female and her children (Buss, 1994). Indeed, they are thought to be more important than physical traits in the consideration of long term partners (Townsend & Levy 1990).

Although females are predicted to prefer long term relationships, they do sometimes engage in short term sexual relationships (Gangestad & Simpson, 2000) that may either secure additional resources for themselves and their children, allow them to mate with more physically attractive males to secure better genes for their offspring or when they perceive the potential for the development of a longer relationship. In contrast to long term preferences, female preferences for short term mates are thought to be strongly influenced by physical traits that indicate good genes (Gangestad & Simpson, 2000).

1.9 Acoustic signalling systems in animals

Interestingly, song and other acoustic signals are the traits most often shown to be sexually selected (Andersson, 1994) in animals. A great deal of research suggests that acoustic signals play an important role in courtship and competitive behaviours in many species including insects, anurans, birds, fish and mammals (including primates). The comparative approach provides a powerful tool for testing hypotheses about evolution (Fitch, 2000) and provides a framework for the examination of the human voice as a signal in the context of mating and competition. Here, the acoustic signals of avians (song birds), anurans (frogs), mammals (deer) and non-human primates are briefly reviewed.

1.9.1 Bird Song

Many species of birds have the ability to produce complex, structured songs consisting of a series of brief sounds arranged in a rhythmic sequence (Kelley & Brenowitz, 2002). Birds posses a unique sound-generating structure known as the syrinx that displays considerable structural variation between individuals. Sound production depends on the syrinx and other respiratory muscles. Bird song is controlled by a network of interconnected nuclei in the forebrain referred to as the song control system. The development of this system is strongly influenced by the sex-steroid hormones. Circulating hormone levels (especially testosterone) generally correlate with singing activity (Prove, 1974) with many temperate zone species only producing song during the breeding season.

For many years it has been known that the males of many songbird species use song to attract female mates (Darwin, 1871) and in contests between males (White, 1789). It is also important in mediating dominance behaviour (Kelley & Brenowitz, 2002). In some avians there are different types of song with different functions. For example, in Parulid warblers two distinct song types appear to be directed at rivals and females of the species respectively (Morse, 1970; Lemon et al. 1987; Kroodsma et al, 1989). In the aquatic warbler *(Acrocephalus paludicola)* there appears to be three types of song, one used in short-range threat, another as a long-range territorial signal, and the third for courtship (Catchpole & Leisler, 1989). Various properties of song are thought to play a role in attracting females; these include song rate, repertoire size and song complexity; whilst song phrase length and repertoire size are thought to be important in territorial defence.

1.9.2 Frog calls

Frog calls are generated by the larynx and are sexually dimorphic. The male larynx is under the influence of androgens during early postmetamorphic development. Male frogs use distinct calls (rapid, prolonged trills) to attract females to the breeding site and also as part of aggressive displays towards other males. The auditory channel is thought to be utilized by frogs because loud sounds can be effectively broadcast over long distances, and also attract attention at night, which is when frogs copulate (Kelley & Brenowitz, 2002). Frog song may contain several important pieces of information. The amplitude (loudness) and pitch of the call are good indicators of both age and size, since older frogs are larger and produce louder and lower frequency calls. Older, larger frogs advertise the ability to successfully survive the environment their offspring will face. Long calls may also provide information about the health of an individual since calling is a physically demanding behaviour.

1.9.3 Red deer roars

Considerable attention has focussed on the role of roaring in northern European red deer (*Cervus elaphus*) upon female choice and aggressive interactions with other males (Clutton-Brock & Albon, 1979; McComb, 1987, 1991; Clutton-Brock, 1988; McElligot & Hayden, 1999). During the breeding season or rut (in late September or early October) red deer stags roar loudly and repeatedly not only towards other stags but also towards hinds that they herd into their harems. The roar is a powerful, low-pitched, groaning sound made only by males and is achieved by retraction of the larynx from its already low resting position (Fitch & Reby, 2001). The period of vocal activity lasts approximately 4-5 weeks during which the roaring rate is highly variable. Clutton-Brock and Albon (1979) propose that stags use roaring contests to assess each others fighting ability in order to avoid potentially costly physical confrontation since roaring rates are highly correlated with fighting ability. Hinds are thought to use the roaring rate of such contests between males to choose which harem to join since it provides a reliable indicator of the quality of the stag (Clutton-Brock et al, 1982).

In a study in which the fundamental frequency of stags was manipulated McComb (1991) observed no effect on female mate choice. However, stags with large body size and large vocal tracts (low formant frequencies) enjoy the highest reproductive success (Reby & McComb, 2003).

Comparative research on red and fallow deer (Fitch & Reby, 2001) and other mammals have shown that a descended larynx is not unique to humans. Since the evolutionary significance of a descended larynx is obviously unrelated to speech in deer Fitch and Reby (2001) propose that the biological function of a descended larynx (that elongates the vocal tract and therefore lowers formant frequencies) is to exaggerate the impression of size.

1.9.4 Non human primates

Vocalisations are an important mode of communication for most non human primate species particularly when visual communication is compromised, for example, in dense forest habitats. However, research relating vocal communication to sexual selection is in its infancy in comparison to that undertaken in other taxa (eg birds, frogs and deer reviewed here) since attention has primarily focused on the comparison between primate communication and human language. There are sexually dimorphic calls in many primates, for example, the loud roars of male howler monkeys (*Alouatta palliate)*, the long calls of male orangutans (*Pongo pygmaeus)* and the more complex male song of gibbons (*Hylobates agilis* and *mueller*s). Several studies suggest that male primate vocalisations function to keep groups separate. For example, male black howler monkeys (*Alouatta caraya*) produce loud calls particularly at around dawn (from which the genus gains its common name) which are thought to regulate the use of space by advertising occupancy serving to settle disputes without chases or fights (da Cunha & Byrne, 2006). This intergroup spacing function indicates intrasexual selection (da Cunha & Byrne, 2006). There is also some evidence in several species of langur that loud calls serve to defend mates by deterring strange males (eg. Van Schaik et al. 1992).

At the present time there is little evidence that male vocalisations are directly involved in mate attraction (Snowdon, 2004) although there is some evidence that female vocal signals influence mating behaviour. For example, female Barbary macaques produce acoustically distinct calls during copulation that vary at different stages of the ovulatory cycle that are thought to both attract males and incite competition between males (Semple & McComb, 2000).

The basic mechanism of voice production in humans and non-human primates is the same, however, there are a number of important morphological differences (Fitch, 2000; 2003). For example, several species of monkeys possess extended vocal membranes not present in humans (Schon Ybarra, 1995) which are thought to enable high pitched vocalisations (Fitch, 2003). Many primates also possess air sacs in the larynx that may be involved in loud calls (Schon Ybarra, 1995; Fitch, 2003). The most important difference is that the adult human larynx is much lower than in other primates (Fitch, 2000; 2003).

1.10 Sexual selection in communication

In a review of the primate literature relating to communication signals Snowden (2004) suggested five criteria for demonstrating sexual selection in communication:

a) **Sexual dimorphism**

   Sexually selected traits usually display sexual dimorphism although it is not a sufficient condition for sexual selection alone. Snowdon points out that a trait may be sexually dimorphic but not sexually selected, for example, in those primates in which low fundamental frequency is related to large body size, low fundamental frequency may not be sexually selected unless other conditions are met (see below).

b) **Variation in the signal between same-sex conspecifics**

Selection of any type can only act on traits that are variable within a population.

c) **Discrimination and preference or avoidance.**

Variance in the trait must be able to be perceived by conspecifics. For intersexual selection to be demonstrated there must be a correlated preference by the opposite sex for part of the distribution of the trait and for intrasexual selection to de demonstrated same sex individuals should seek to avoid the signaller.

d) **Expression of preference (or avoidance) in the context of mating**

In order for a trait to be sexually selected it should bear a relationship to reproduction either by attracting opposite sex mates or repelling same sex rivals. Snowdon (2004) suggests that an ideal signal for sexual selection should communicate something about reproductive condition and be effective when reproduction is possible.

e) **Outcome of preference (or avoidance) must relate to reproductive success**

The expression of the preference or avoidance should result in differential reproductive success.

1.11 The Human Voice

Acoustic cues are sexually selected traits that play an important role in courtship and competitive behaviours in many animals. However, the examination of the role of the human voice within this context is a relatively new field of research and is the focus of this thesis. In most animals signalling is specialised, however, the signals studied in human vocalisations occur in all voiced speech. In order to examine the role of the voice in human attraction and competitive behaviours some basic knowledge of vocal production and voice perception is necessary.

1.11.1 Human vocal production

The vocal process involves the larynx (the 'voice box') that generates sound and the resonating chambers of the vocal tract including the pharynx and the oral and nasal cavities that modify the source sound (see Figure 1). According to the Source-Filter Theory of Speech Production (Fant, 1960), fundamental frequency is determined by the vibration of the vocal folds (the source) and formants are determined by the size and shape of the vocal tract (the filter) and by moving the articulators (the tongue, lips and soft palate etc.) (Fitch, 2000).

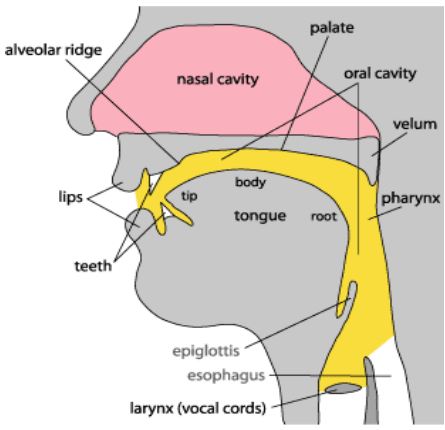


Figure 1a - Diagram of the vocal tract (Source: www.indiana.edu/ VocalTractLabels.gif)

Any sound production system consists of three components: an air-generating mechanism, a vibrating mechanism and a resonating cavity (Hauser, 1996).

1.11.2 The air generating mechanism

The energy source for human speech is air exhaled from the lungs.

1.11.3 The vibrating mechanism

The larynx is the sound generator in human voice production. Located in the neck, it is composed of a skeleton of cartilages, ligaments and small muscles. When speaking, air is forced through the vocal folds in the larynx causing them to vibrate. The vocal folds (or cords as they are commonly known) connect the thyroid cartilage (the Adam's apple) at the anterior of the larynx to the mobile arytenoicartilage at its posterior (see figure 1b for an illustration of normal vocal cords). The arytenoid cartilages in the larynx bring the vocal folds together in a process called adduction (the opposite process is known as abduction). Air is forced through a V-shaped opening called the glottis between the vocal folds causing them to vibrate. This causes the steady stream of air from the lungs to be transformed into a series of puffs of sound producing voiced speech. When the vocal folds do not vibrate the sound is considered 'voiceless'. The rate of vibration or oscillation of the vocal folds determines fundamental frequency and its harmonic components (integer multiples of the frequency) (Titze, 1994) which are the primary determinant of the perceived 'pitch' of a vocalization. If the vocal folds are vibrating 200 times a second they are said to be vibrating at 200 Hertz (Hz).

Figure 1b: Normal vocal folds during silence (Source: NYU Medical Centre - www.med.nyu)

Fundamental frequency can be derived from the length, density and stress of the vocal folds and may be predicted from the equation:

Equation: $F = \frac{1}{L}\sqrt{\frac{\sigma}{\rho}}$

Where F= fundamental frequency, L = the vocal fold length, σ = the longditudinal stress on the vocal folds and p = the vocal fold density (Titze et al., 2000).

Thus, fundamental frequency is inversely proportional to vocal fold length and directly proportional to the square root of tension on the vocal folds. Generally, longer vocal folds with less tension produce lower fundamental frequencies. Baken (1987) suggests the following typical ranges of fundamental frequency in humans:

Adult male: 85-155 Hz

Adult female: 165-255 Hz

Child (aged 10): 208-259 Hz

Infant (12 months): 247-410 Hz

1.11.4 The resonating cavity

Acoustic energy then passes through the vocal tract (the pharynx and the oral and nasal cavities) where some of the frequencies are removed entirely and some resonate more than others depending on the size of the areas in the vocal tract determining the formants (or resonances). Theoretically there are an infinite number of formants and it is possible to measure at least six formants in humans but only the first three are necessary for phonetic distinctions to be preserved (Fitch, 2002). The two largest spaces in the vocal tract are the throat and mouth so that they produce the lowest formants. F_1 - the throat and F_2 - the mouth. It is the formant frequency (abbreviated from formant centre frequency) of the formant and the overall pattern of these frequencies that is perceptually important in human speech. Differences in the first three formants allow the vowel sounds of speech to be distinguished. Because of their resonant origin they tend to stay essentially the same when fundamental frequency is changed. Benade (1990) suggests the following ranges of frequencies for the first four formants of an adult male voice:

1st formant: 150-850 Hz

2nd formant 500- 2500 Hz

3rd formant 1500-3500 Hz

4th formant 2500-4800 Hz

The formant frequency for any given length of acoustical tube can be derived from the formula below:

$$F = \frac{c}{4L}$$

Where F = formant frequency, *c* = the speed of sound and L is the length of tube.

A tube resonates with maximal amplitude a sound whose wavelength is four times the length of the tube. If the tube is open at one end and closed at the other as most closely approximates the human vocal tract (closed at the glottis and open at the mouth) formants occur in multiples. The expression (2n-1) is used to generate odd number integers and allows the derivation of formant frequencies for this type of open at one end tube:

$$F1 = \frac{c}{4L} \qquad F2 = \frac{3c}{4L} \qquad \text{and so on} \ldots$$

Higher formants can be determined by continuing the calculations for (2n-1). Although the open at one end model provides an approximation of the human vocal tract, the glottis actually opens and closes many times during speech. Since the average distance between the formants remains the same whether the vocal tract is open or closed at the glottis the measure of formant dispersion, the average distance between successive formants (Fitch, 1997) is therefore often used as a measure to avoid different estimates depending upon the position of the glottis at the time of measurement.

Although the term ‘formant frequencies’ is unknown to most lay people and they are often confused with fundamental frequencies, they have been described as the single most important acoustic parameter in human speech (Fitch, 2000). Generally, longer vocal tracts produce lower, more densely spaced formant frequencies (there is less formant dispersion).

1.11.5 The Independence of source and filter

It is important to note that fundamental frequency and formant frequencies are independent of one another in human speech - “*their independence is one of the central tenets of modern speech science*” (Fitch, 2002). Whilst the concept of pitch is easily understood, formants are more difficult to conceptualize. They are one component of ‘timbre’ or ‘voice quality’ and are highly audible and salient (Fitch, 2000). Formants can vary independently of the source and formants have little or no influence on the perception of pitch (Fitch & Hauser, 1995). An interesting demonstration of their independence comes from what Fitch and Hauser (1995) referred to as “Donald Duck” speech after inhaling helium from balloons. Because heliox (a mixture of helium and oxygen) increases the speed of sound in air and formants depend upon the transit time of sound waves up and down the vocal tract; raising the speed of sound by inhaling heliox shortens the transit time and nearly doubles formant frequencies without shifting fundamental frequencies appreciably.

1.11.6 The ontogeny of the human voice

In most mammals and human newborns the larynx is high in the throat so that respiratory and digestive pathways are largely separate allowing simultaneous nasal breathing and swallowing (Crompton et al. 1997). The high position of the larynx severely limits the repertoire of vocalisations human babies can produce (Lieberman, 1984). However, in the first few months of life the larynx slowly begins to descend but continues to remain high in the neck until a major qualitative change in position occurs probably between the second and third years of life (Laitman & Reidenberg, 1993). By the third year the larynx has significantly lowered in the larynx and the respiratory and digestive tracts intersect in the area of the pharynx creating a common digestive and respiratory pathway. The descent of the larynx expands the supralaryngeal portion of the pharynx allowing greater modification of the sounds produced by the vocal cords and therefore a wider range of vocalisations in adult humans (Laitman & Reidenberg, 1993).

The emergence of the descended larynx in human evolution is controversial. Laitman and Reidenberg's studies of fossil basicrania (the base of the cranium) suggest that it arrived with the emergence of our own species *Homo sapiens* some 300,000-400,000 years ago. This proposal is based on the observation that a flat basicranium (possessed by most mammals) indicates a larynx that sits high in the neck whilst an arched cranial base signifies a lower larynx. *Homo erectus* display bending and flexing of the basicranium comparable to that of a 6 year old whereas *Homo sapien* specimens display a fully flexed (angled) adult basicrania. The emergence of the descended larynx in humans remains a hotly debated topic and is likely to remain so since the vocal tract is largely made up of soft tissue which does not fossilize.

There are small differences in boys and girls voices prior to puberty (Whiteside & Hodgson, 2000) and judges are able to discriminate between the voices of pre-pubescent boys and girls (Sachs et al, 1973). Boys are reported to have slightly lower formants than girls (Sachs et al, 1973, Lee et al, 1999).

Pubertal changes that take place in the larynx are thought to be under the influence of testosterone in males and in females under the influence of oestrogen and progesterone (Jenkins, 1988). The male voice begins to 'break' when serum testosterone levels reach approximately 10nmol/l and SHBG (sex hormone binding globulin) drops (Pedersen et al., 1986)

Under the influence of dihydrotestosterone (a metabolite of testosterone) the vocal folds in the human male lengthen by up to 63% and permanently thicken (Jenkins, 1988) resulting in a lowering of fundamental frequency. In comparison, female vocal fold growth is only 34%. Physiological changes to the vocal folds result in an average fundamental frequency for an adult male of approximately 100 Hz, while it is around 213 Hz for an adult female (Muller, 1948).

A simultaneous but independent secondary descent of the larynx also takes place during puberty and is much greater in males than females. A magnetic resonance study of a large number of participants from 2.8 to 25 years of age revealed that the average vocal tract length diverged significantly between males and females after 15 years of age; postpubertal males showed a vocal tract averaging 12.9mm longer than females (Fitch & Giedd, 1999). There is also a gradual change in the shape and axis of the larynx including growth of the thyroid cartilage which produces the prominence known as the Adam's apple. The descent of the larynx increases the length of the vocal tract, lowering formant frequencies and creating less formant dispersion (the formants are closer together). Generalised somatic growth (under the influence of growth hormone, gonadal steroids and genes) results in an increase in size of the resonance chambers in both men and women that also contributes to the increased resonance and power of the adult voice (Jenkins, 1998). The exact mechanism for the descent of the larynx remains unknown. Testosterone is thought to play a role although other factors are likely to be involved including growth hormones (Fitch & Giedd, 1999). Fitch and Giedd (1999) proposed that the secondary descent of the larynx in human males represents a sexually dimorphic adaptation to give adult males a more imposing voice relative to females and prepubescent males. Fitch's size exaggeration theory suggests that formant frequencies may play an important role in male-male competition for mates.

The influence of testosterone at puberty on the human voice is illustrated by a unique historical practice. In the late 16th Century, castration prior to puberty began to be practiced by the Church of Rome in order to produce a highly prized adult male soprano voice known as 'castrati'. The quality of the castrato voice is achieved by pre-pubertal vocal folds (undeveloped due to the absence of testosterone) but with the power of the adult male physiology (Jenkins, 1998; Abitbol et al, 1999), including large resonating chambers and a normal male vocal tract. Jenkins (1998) reports that in the only known post-mortem examination of a castrato the dimensions of the larynx were strikingly small and that the vocal cords were the length of a female soprano.

Similarly the voices of males with hypogonadal disorders in which the production of testosterone is markedly impaired such as Klinefelter syndrome, Kallman syndrome and idiopathic hypogonadotropic hypogonadism (IHH) do not 'break'. In such conditions there is also development of eunchoidal body proportions which includes exceptionally tall stature (because of retarded closure of the epiphyseal lines of the bone extremities) and a feminine fat distribution (Nieschlag & Behre, 2004). Testosterone treatment for male hypogonadism is known to permanently lower the fundamental frequency of male patients (King et al., 2001; Akcam et al., 2004) and following an injection of testosterone in females irreversible masculine vocal characteristics are produced (Vuorenkosi et al., 1978). Under the greater influence of androgens following the hormonal shift at menopause when oestrogen and progesterone levels drop but testosterone levels may remain the same, the voices of post-menopausal women may also deepen (Abitbol et al., 1999) by about 15Hz by the age of 70. (Stoicheff, 1981; Pegoraro-Krook, 1988). A similar lowering of fundamental frequency can also be induced by smoking (Gilbert & Weismer, 1974).

In an unpublished pilot study carried out with colleagues at Northumbria University a sample of 18 homosexual males (mean age = 23.5) were found to have significantly higher fundamental frequency (mean = 110 Hz) than a sample of 23 heterosexual males (mean = 100.50 Hz) although no difference in formant dispersion was observed.

In conclusion, few changes are thought to occur in the human voice following the major qualitative changes that occur during puberty although the voice may be deleteriously affected by general ageing processes such as atrophy of soft tissues.

1.12 Auditory Perception

According to Stevens (1998) sound waves travel down the auditory canal to the eardrum (tympanum) causing it to vibrate. The ossicle bones then amplify and transmit sound waves to the basilar membrane of the inner ear (cochlea). Different parts of the basal membrane are most responsive to certain frequency ranges and they are arranged tonotopically (Robels & Ruggero, 2001). The cochlea acts like a spectrum analyzer converting the sound waves to electrical impulses which travel down the auditory nerve to the auditory centres of the brain.

The voice is the most important sound in our auditory environment (Belin et al, 2004) since accurately perceiving the information contained in vocalisations is of critical importance to the social interactions and survival of all animals including humans. Current research is examining whether voice perception may involve specialised mechanisms not used for other, non-vocal, sounds.

For example, Belin et al. (2000) used functional magnetic resonance imagery (fMRI) to measure activity during perception of vocal and non-vocal natural sounds. Highly selective, discrete regions of the auditory cortex (the superior bank of the superior temporal sulcus or STS) were found in both hemispheres that exhibited a greater response to vocal sounds than control sounds whereas no areas were found that responded more greatly to non-vocal sounds than vocal sounds. A second study by the same authors (2002) found that the right anterior STS had a significantly stronger response to non-speech vocalizations than to scrambled versions of the same stimuli (Belin et al., 2002). Additional research has observed a ‘voice-specific response’ (VSR) when examining the difference between sung voices and musical instruments using electrophysiological techniques (Levy et al, 2001; 2003). An interesting study by Gervais et al. (2004) on a small group of autistic adults (n=5) showed no difference between groups for the control (non-voice) sounds but that autistic participants did not show additional STS activation for voice sounds, instead, the pattern observed was similar to that for non-voice sounds. These findings are consistent with the behaviour of autism and findings of similar abnormal activation of face-processing networks in autism (Schultz, 2000). There is therefore converging evidence that cortical areas of the human brain are selectively activated by the human voice (Belin, 2006) in much the same way that face-selective regions are thought to exist in the visual cortex (Puce et al, 1995; Kanwisher et al., 1997; Haxby et al., 2001).

Recent neuroimaging research has also examined the areas of the brain responsible for more finely tuned perception of the specific acoustic properties of voices – fundamental frequencies and formant frequencies - suggesting different cortical areas may also be responsible for their perception, with dissociations in the right hemisphere (Hall et al., 2003; Lattner et al., 2005) or perhaps even hemispheric differences (Zatorre et al., 2002). The study by Lattner et al. (2005) suggests a functional segregation of the right hemisphere with fundamental frequency predominantly processed by mid superior temporal gyrus (STG) areas (anterior to Heschl's Gyrus) and formants processed by overlapping areas in the posterior STG and inferior parietal lobe (IPL).

Chapter Summary

According to evolutionary theory, sexually dimorphic traits may be modified by evolution through the process of sexual selection to attract mates (intersexual selection) and to intimidate rivals (intrasexual selection). Vocalisations are known to play an important role in both courtship and competitive behaviours in many animal species. Following puberty the human voice is sexually dimorphic with males having a considerably deeper voice due to changes that take place in the larynx. Two independent acoustic components combine to produce the deepest voice in human males – low fundamental frequencies and low formant frequencies. A deep voice is therefore a sexually dimorphic trait emerging at sexual maturation and is dependent (at least in part) upon the sex hormones; it is thus a likely candidate for sexual selection.

CHAPTER 2

Vocal frequency and physical measures

Note: Aspects of this chapter have been published in Evans, S., Neave, N. & Wakelin, D. (2006). Relationships between vocal characteristics and body shape in human males: an evolutionary explanation for a deep male voice. Biological Psychology. 72, 160-163.

Acoustic signals are known to play an important role in courtship and competitive behaviours in many animals and relationships between acoustic parameters and aspects of body size, age and hormonal status have been reported in many species (Appleby & Redpath, 1997; Ballintijn & ten Cate, 1997; Fusani et al, 1994). In order to attempt to understand how aspects of the human male voice may be involved in courtship and competitive behaviours in humans, the first two studies in this research programme examine whether the two independent components of the voice (fundamental and formant frequencies) may provide honest signals of physical attributes such as body size, body shape, age and hormonal status in male humans. The current chapter examines the relationship between vocal parameters and physical attributes and age. An examination of the relationship between these same acoustic properties and hormonal status follows in chapter 3.

STUDY 1

2.0 Study 1 - Rationale

A relationship between body size and acoustic parameters is commonly found in many animal species (Appleby & Redpath, 1997; Giacoma et al., 1997) including primates (Hauser, 1993); with larger individuals producing lower frequency sounds (Morton, 1977; Howard & Young, 1998). However, although human listeners appear to use acoustic cues to make inferences about the age and physical characteristics of a speaker, there is conflicting evidence as to whether vocal parameters are reliable indicators of such physical characteristics in humans.

In the past it was commonly thought that fundamental frequency was an indicator of body size in adult human males. As early as 1872 Darwin proposed a link between body size and fundamental frequency, although subsequent studies failed to find a relationship (Kunzel, 1989; Lass and Brown, 1978; Sawashima et al., 1983). However, fundamental frequency has been demonstrated to be negatively related to height as a function of age in pre-pubertal males (Heber et al., 1999)

Fitch and colleagues have proposed that formant dispersion rather than fundamental frequency forms an acoustic cue to body size. There is indeed evidence of a correlation between body size, vocal tract length, and formant frequencies in non-human primates (Fitch & Giedd, 1999). Fitch (1997) found a strong correlation between formant dispersion and body size in 23 rhesus macaques, the formant frequencies of larger individuals being closer together. Using magnetic resonance imaging Fitch and Giedd (1999) also found a strong positive correlation between body size and vocal tract length in a study of 129 male and female humans.

A study by van Dommelen and Moxness (1995) examined the ability of both male and female listeners (10 males and 10 females) to judge the height and weight of male and female speakers from speech samples (isolated words and paragraphs). They found that male judges' estimates of male physical characteristics corresponded quite well with actual height and weight. However, female listeners were much less successful at estimating male height and weight and listeners of both sexes were unsuccessful at estimating female height and weight. Low fundamental frequency, low formant frequencies and slow speech rate was taken to indicate large male body dimensions although only male speech rate was correlated with actual weight (heavier men having a reduced tempo). The discrepancy between the success of male and female listeners success at accurately judging size from vocal cues is interesting. One possible explanation is that human males but not females commonly use vocal cues to assess the size of other males in the context of intrasexual selection.

In a study by Collins (2000) men with deeper voices were judged as being taller, older, more likely to have a hairy chest and a muscular body type by 54 female listeners. Once more the female judges were inaccurate, their estimates did not predict the actual height, age, amount of chest hair and musculature of the male speakers although estimates of weight did predict the actual weight of the speaker. No relationship between any acoustic and any of the physical parameters measured was found.

However, Gonzalez (2004) examined the relationship between various acoustic measures and height and weight in a large sample of both males and females, using samples of vowel sounds and running speech. Here a weak correlation between measures of formant frequencies (but not fundamental frequency) and height and weight was found within sex. The relationship was stronger in females than males.

Since past evidence for a relationship between vocal frequencies and physical characteristics in human males is conflicting, the current correlational study aimed to re-examine this relationship. For the purposes of this investigation a distinction was made between body size (height and weight) and body shape (measures of circumference and measures derived from these measures such as shoulder-hip-ratio). The prediction was that formant frequencies would be related to height and weight in line with the findings of Gonzalez (2004) and that, since both fundamental frequency and aspects of body configuration are dependent on testosterone, that fundamental frequency may indicate aspects of body configuration rather than body size. Although Collins (2000) found no relationship between vocal parameters and some measures of body shape, the current study aimed to re-examine this relationship using a wider range of physical measures.

2.1 Study – 1 Materials and methods

2.1.1 Participants

Participants were recruited on a voluntary basis from an opportunity sample at the Northumbria University campus and the general population. 50 self-reported heterosexual males aged between 18-68 (mean = 29.08, sd = 12.31) took part in the study. All participants reported that they had not suffered any damage, or had surgery to their nose or throat or broken any bones associated with the physical measures taken. English was the first language of all participants.

2.1.2 Materials

Measures of vocal characteristics and analysis

All voices were recorded using a PC with a Logic headset microphone onto Steinberg WaveLab 5.0 software. The headset microphone ensured that all speakers were at a constant distance from the microphone (10 cms) when recording was taking place and a constant sound recording level was used. Each participant was asked to repeat the English vowels “A”, “E”, “I” and “O” replicating the method used by Collins (2000). Praat software v.3.9.2 (Boersma & Weenink, www.praat.org) was used for vocal analysis. The mean fundamental frequency of the middle of the vocal sample was calculated (to avoid noise at the beginning and end of the sound) using the autocorrelation method (analysis parameters were modified for adult male - minimum pitch 75 Hz/Maximum pitch 300 Hz). Mean values for Formants 1-4 were calculated for both vocal samples using the Burg Linear Predictive Coding Algorithm (default parameters were used except maximum formant was modified to 5000 Hz suitable for adult males). Formant dispersion was calculated as (F3-F2)+(F2-F1)/2 (as in Feinberg, 2005) because the fourth frequency was not present in all individuals and in order to provide a single formant measure for analysis.

Physical measures

Physical measures were taken using an anthropometric body measurement tape. Skull circumference (circ.) was measured above the eyebrow; neck circumference was measured around the neck at the laryngeal prominence (Adam's apple); shoulder circumference was measured at the widest point of the shoulders between the acromion bones with the individual's arms at their side. Chest circumference was measured at the widest point; waist circumference was measured at the level of the umbilicus and hip circumference was measured at the greatest girth around the hips and buttocks. Height was measured using a stadiometer and weight using digital scales. Shoulder-Hip Ratio (SHR), Shoulder-Waist Ratio (SWR), Waist-Hip Ratio (WHR) and Body Mass Index (BMI) were derived from these measurements. A measure of maximal peak expiratory flow (PEF) was taken using a spirometer as a measure of lung capacity.

2.1.3 Procedure

All participants gave their informed written consent and the procedure was passed by the School of Psychology & Sport Sciences Ethics Committee. Participants were tested individually and firstly asked to complete a brief, biographical questionnaire. All physical measurements were then taken as well as measures of height, weight and lung capacity. The participant's voice was recorded before the participants were debriefed.

2.2 Study 1 - Results

2.2.1 Descriptive Statistics

Results of the vocal analysis found that the mean fundamental frequency of the vocal samples was 106.54 Hertz (Hz) (SD =16.21) with a range of between 75.54 Hz and 159.55 Hz. The mean formant dispersion was 1651.71 Hz (SD = 88.09) with a range of between 1497.79 Hz and 1720.78 Hz. Table I provides a summary of the mean, standard deviation and range of the physical measures taken. The physical measures were comparable to those found in other studies where comparisons could be made (Hughes et al., 2004; Gonzalez, 2004).

Measure	**Mean**	**SD**	**Range**
Body Size:			
Weight (kg)	81	12.94	62.70-111.20
Height (cm)	179.82	6.22	165-195
Body Mass Index	27.27	7.48	18.93-54.27
Peak Expiratory Flow (l/min)	466.50	144.15	84-775
Body Shape:			
Skull circ. (cm)	57.99	1.59	55-62
Neck circ. (cm)	38.92	2.32	34-46.5
Shoulder circ. (cm)	108.78	7.60	96-129.5
Chest circ. (cm)	96.79	8.74	82-117
Waist circ.(cm)	89.74	11.18	74-114
Hip circ. (cm)	99.29	7.48	84-115
Shoulder-Hip Ratio	1.10	.08	1.07-1.14
Shoulder-Waist Ratio	1.12	.12	1-1.17
Waist-Hip Ratio	1.12	.12	1.01-1.14

Table 2a - Mean, standard deviation and range of the physical measures taken.

2.2.2 Correlations

Pearson Product-Moment Correlations were carried out using SPSS software (v.12.0.1) for mean fundamental frequency, formant dispersion and age. A significant positive relationship was found between fundamental frequency and age of participant ($r = .43$, $p = .002$). Younger individuals had lower fundamental frequency (see figure 2a). No significant relationship was found between age and formant dispersion. Since age was identified as a possible confounding factor, all further analyses of fundamental frequency were carried out using partial correlations (r_p), holding age constant. See Appendix III - Tables 2b & c for correlation matrices.

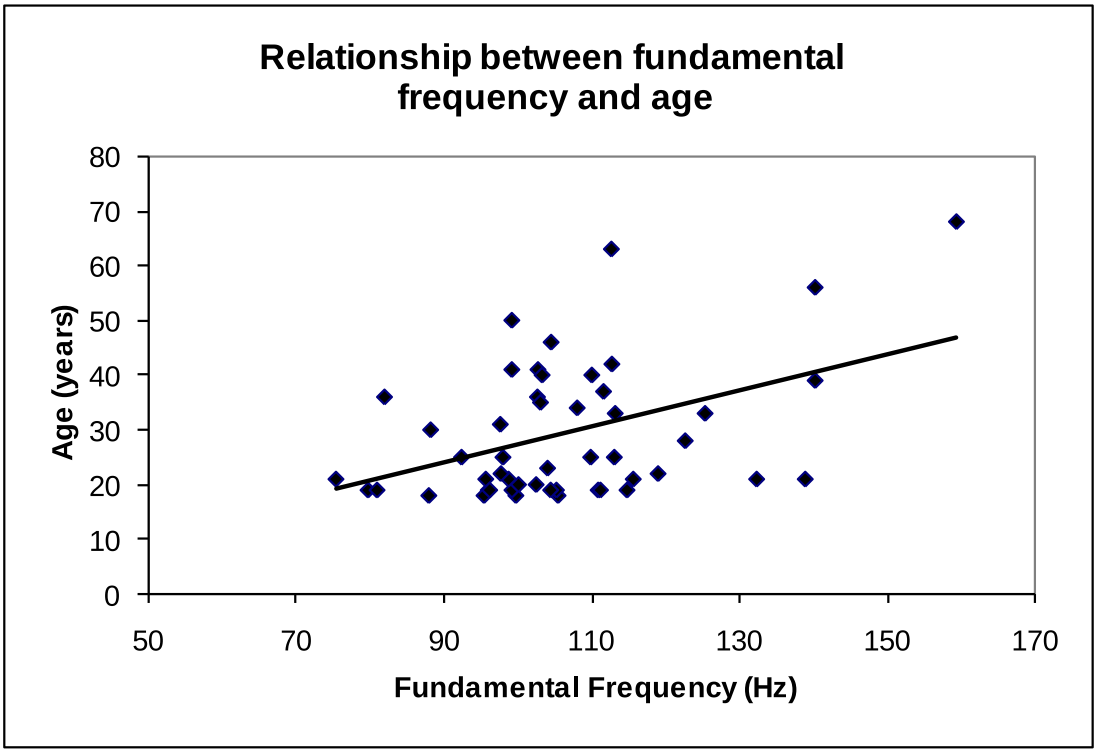


Figure 2a – Relationship between age and fundamental frequency

With regard to body size, no significant relationship was found between the mean fundamental frequency of the vowels and height, lung capacity or Body Mass Index although weight was significantly negatively correlated to mean fundamental frequency (r_p = -.34, p=.02), heavier individuals had lower fundamental frequency. Weight and height were significantly negatively correlated with formant dispersion, (r = -.43**,** p = .002; r = -.32, p = .024 respectively) demonstrating that heavier and taller individuals had smaller formant dispersion. No significant relationship was found between formant dispersion and Body Mass Index or lung capacity.

With regard to body shape, no significant relationship was found between mean fundamental frequency and skull, neck, waist and hip circumferences. However, shoulder circumference was significantly negatively correlated with mean fundamental frequency, (r_p = -.29, p = .04) and chest circumference was significantly negatively correlated with mean fundamental frequency, (r_p = -.28, p= .04. Shoulder-Hip Ratio was also significantly negatively correlated with mean fundamental frequency, (r_p = -.49, p <.001) Larger shoulder and chest circumference as well as Shoulder-Hip Ratio indicated lower fundamental frequency. No significant relationship was found between Waist-Hip Ratio, Shoulder-Waist Ratio and mean fundamental frequency.

No significant relationship was found between skull and hip circumferences and formant dispersion. However the following circumferences were significantly negatively correlated with formant dispersion: neck, r = -.50, p

<.001; shoulder, r = .-56, p <.001; chest, r = -.45, p =.001 and waist, r = -.39, p = .005. Larger circumference indicated smaller formant dispersion. Shoulder-Hip Ratio was also significantly negatively correlated with formant dispersion (r = -.39, p = .006) although there was no significant relationship between fundamental frequency and Shoulder-Waist Ratio and Waist-Hip Ratio.

2.3 Study 1 - Discussion

Results of the current study revealed that fundamental frequency but not formant dispersion was related to age; younger (but post-pubertal) males had lower fundamental frequency. In line with the prediction, this study found a significant negative relationship between the fundamental frequency of the male voice and various measures of body shape including shoulder and chest circumferences and Shoulder-Hip Ratio. Lower fundamental frequencies indicated individuals with a larger body shape, specifically in terms of upper body musculature. Fundamental frequency was also related to one measure of body size; weight was significantly negatively correlated with fundamental frequency. Further, a stronger significant negative relationship was also found between formant dispersion and body size (weight and height). Interestingly, a relationship was also found between formant dispersion and body shape (neck, shoulder, chest and waist circumferences and Shoulder Hip Ratio). Smaller formant dispersion indicated males with a larger body size and shape.

First, with regard to body shape and fundamental frequency, findings of a relationship between low fundamental frequency and large body shape, a large upper musculature, suggests that a speaker’s fundamental frequency provides a cue to body configuration. Low fundamental frequency and sexually dimorphic body configuration are both determined at puberty by the action of testosterone and may therefore be honest multi-channel signals of genetic quality and hormonal health to female mates.

Second, with regard to formant frequency and body size, Gonzalez (2004) found a weak relationship between formant frequencies and height and weight and Sachs et al. (1972) found a negative correlation between vowel formant frequencies and height. The current study supports these findings although the correlation between formant frequencies was stronger for weight than height.

Both Gonzalez (2004), and the current study, found a weaker relationship between body size and formant frequencies in humans than Fitch (1997) found in rhesus macaques. One possible explanation of a weaker relationship between formant frequency and body size in humans than other primates is that the secondary descent of the larynx in human males disassociates vocal tract length from skeletal and body size (Fitch, 1997). Indeed, Gonzalez (2004) found a stronger relationship between formant frequencies and body size in women than males, supporting this proposal.

Thirdly, the current study also found a correlation between formant dispersion and body shape not previously reported. Body shape or SHR and fundamental frequency are known to be largely dependant on levels of testosterone present at puberty. The control mechanism by which the larynx is lowered in human males is currently unknown, however these results imply that testosterone may also play a role here although it is most likely that these changes in the larynx are under the influence of an interaction between both sex and growth hormones as suggested by Fitch (1997).

Finally, once the age of participant was controlled for, the current study involving English speaking males found a correlation between fundamental frequency and weight not previously reported. However, the relationship between weight and formant dispersion and fundamental frequency must be viewed with caution, since the prevalence of overweight individuals in Western society may weaken any correlation (Fitch, 1999).

Examination of the graph displaying the relationship between age and fundamental frequency (Figure 2a) suggests that there may have been outliers in the data set. Whilst an outlier analysis could have been performed, there was no valid reason to exclude data on the grounds that there were no particularly unusual values for any variable given the wide age range of the participants.

Chapter Summary

To attempt to understand how aspects of the human male voice may be involved in courtship and competitive behaviours in humans the first study of this thesis investigated whether these acoustic parameters

were related to both physical measures and age in human males. Results suggested that relationships between physical and acoustic parameters in human males do exist. Fundamental frequency was found to be related to age, and both fundamental and formant frequencies were related to aspects of both body size and shape. It is therefore plausible that the human male voice provides an acoustic signal of such attributes to potential female mates and male rivals. The question of why such acoustic cues would be necessary when in most (although not all) situations the listener is probably able to see the speaker is addressed later in this thesis.

CHAPTER 3

Is the voice an honest signal of hormonal quality?

Note: Aspects of this chapter have been published in Evans, S., Neave, N., Wakelin, D. and Hamilton, C. (2008). The relationship between testosterone and vocal frequencies in human males. Physiology & Behavior. 93, 783-788.

The previous study demonstrated that aspects of the human male voice are related to age and various measures of body shape and size but do fundamental and formant frequencies also reflect hormonal status? It is thought that sexual dimorphism of the male voice which primarily occurs during puberty is (in part at least) under the influence of the sex steroid hormone testosterone. There is also some evidence that vocal parameters remain correlated with circulating levels of testosterone in adulthood suggesting that the voice may provide an honest signal of hormonal quality. Thus the second study in this thesis seeks to further investigate this relationship, and also examines the putative relationship between prenatal testosterone (as measured by 2D:4D ratio) and male vocal parameters. In addition, any relationship between salivary cortisol and male vocal frequencies are also explored.

3.0 Study 2 - Rationale

Changes in the male larynx during puberty permanently lower both fundamental and formant frequencies contributing to a deeper, more imposing voice in an adult male relative to a prepubescent child or adult female. Vocal frequencies in males may provide honest signals of male physical quality, specifically in relation to body shape and size (see chapter 2) but do they also provide 'honest' signals of hormonal quality?

3.0.1 Circulating testosterone

A small number of studies have investigated the relationship between circulating levels of free testosterone as measured from saliva samples and vocal parameters in human males. For example, Meuser and Nieschlag (1977) reported lower testosterone/estradiol ratios among tenors than baritones and bases. Pedersen et al. (1986) found a negative correlation ($r = -0.35$) between testosterone and fundamental frequency in a small sample of 19 young men; with high testosterone indicating low fundamental frequency. Dabbs and Mallinger (1999) also found a relationship between testosterone and fundamental frequency $r(59) = -0.26$, $p < 0.05$ in a sample of 61 men (mean age 19.7, mean fundamental frequency 99Hz, mean testosterone 9.63 ng/dl). However, although Bruckert et al. (2006) found speakers with small formant dispersion to have higher testosterone $r = -0.39$ in a study of 26 French males (mean age 24.2) they found no relationship between testosterone and fundamental frequency contradicting previous findings.

A pilot investigation was run alongside the first study of this thesis to examine the relationship between circulating testosterone and measures of both fundamental frequency and formant dispersion. 50 self-reported heterosexual males took part in the pilot study (mean age = 29.08 years, mean fundamental frequency 106.26 Hz, mean formant dispersion 1647.68 Hz, mean testosterone 164.96 pg/ml). All provided speech samples from which measures of fundamental and formant frequencies (including formant dispersion) were derived. Samples of testosterone were collected using cotton swabs and salivettes. Concentrations of testosterone in saliva were determined by radioimmunoassay carried out in an in-house laboratory. After controlling for age, no relationship was found between fundamental frequency and testosterone but testosterone was significantly positively related to formant dispersion $r_{(43)} = .330$, $p = .02$). Men with higher testosterone had larger formant dispersion. These results were surprising and contradict previous findings.

Mixed findings combined with some methodological issues in previous studies, including that employed in the pilot study, suggested that a more careful examination of the relationship between testosterone and vocal parameters may be necessary, in particular, a more rigorous measurement of testosterone levels. In addition although there is considerable diurnal variation in testosterone levels (Diver et al. 2003) no previous study has controlled for potential time of day effects. The current study therefore investigated the relationship between circulating levels of free testosterone and both fundamental frequency and formant frequencies in adult males using methodology designed to address some of the issues identified.

3.0.2 Prenatal testosterone

The examination of the relationship between early exposure to testosterone and vocal parameters is incomplete and remains equivocal. The ratio between the second and fourth fingers (2D:4D) has been proposed as a putative marker of prenatal testosterone exposure (Manning, 2002). While it might be assumed that early androgen exposure might have little influence upon adult characteristics determined by circulating androgen levels during puberty, some studies have revealed that early androgen exposure (as assessed by 2D:4D) might be associated with certain physical characteristics determined during puberty, suggesting that these two surges might be related (e.g. Fink et al., 2003; Neave et al., 2003). This measure has been used to assess possible relationships between early prenatal testosterone exposure and vocal parameters in adulthood, but with little success. One study (Putz et al., 2004) found no relationship between a measure of fundamental frequency from continuous speech and 2D:4D ratio. Another study (Hughes et al., 2002) revealed no relationship between subjective measures of vocal attractiveness and 2D:4D ratio. While the evidence thus far appears lacking for a relationship between prenatal androgen exposure and adult vocal parameters, this study reassessed such a relationship to provide further clarification.

3.0.3 Cortisol

Cortisol production and testosterone are inversely related in adult humans and there is evidence to suggest that stress can suppress testosterone production (Cumming, Quigley & Yen, 1983). Cortisol may also have an association with dominance and social rank in both animals and humans. Animals generally show a rise in cortisol following defeat and chronically higher glucocorticoid levels have been observed in subordinate animals of many species (Sapolsky, 1982; Wirth et al, 2006). In humans although there is some evidence of an association between cortisol and social rank, findings are contradictory concerning the direction of such a relationship (Decker, 2000; Bourne et al., 1968; Brandstadter et al., 1991). Of relevance to the current study, is an experiment examining the modulation of vocal behaviour in male and female toadfish (*Opsanus beta*); Remage et al, (2006) found that glucocorticoids regulate vocalizations in non-advertisement contexts. The current study therefore aimed to examine whether there was any relationship between measures of cortisol and vocal parameters in human males without predicting the direction of any such relationship.

3.1 Study 2a

3.1.1 Study 2a - Rationale

Study 2a aimed to comprehensively examine the relationship between circulating testosterone and both fundamental and formant frequencies. Further it also aimed to examine the putative relationship between pre-natal testosterone (as measured by 2D:4D) and vocal frequencies. Finally, the current study provided an opportunity to explore the possibility of a relationship between cortisol and vocal parameters.

3.1.2 Study 2a - Materials and methods

3.1.2.1 Participants

The sample comprised 40 healthy males aged 18-25 (mean = 20.6 years, SD = 1.81) recruited from student population of Northumbria University. All were self-reported heterosexual, non-smokers with English as their first language.

They reported that they were currently not suffering from any chronic diseases or hormonal abnormalities. None were currently suffering from any conditions that might affect their voice (e.g. colds, sore throats etc) and none reported past or current steroid use. The sample did not include any shift-workers since shift work is known to effect secretions of both cortisol and testosterone (Touitou et al, 1990). They were paid £10 for their participation.

3.1.2.2 Study 2a - Procedure

The study received ethical approval by the School of Psychology & Sport Sciences Ethics Committee. During an initial laboratory-based training session, participants gave their written informed consent, completed a brief biographical questionnaire, and their left and right hands were scanned. They then practiced the protocol for providing saliva samples and vocal recordings, and were given the equipment and instructions necessary for them to provide both. As both testosterone and cortisol have been shown to display considerable diurnal variation (Diver et al. 2003; Valero-Politi & Fuentes-Arderiu, 1996), three samples across a single day were collected at 9am, 12 noon and 3pm. Participants returned the voice recorders and saliva samples to the laboratory following the final collection, and were fully debriefed.

3.1.2.3 Finger ratio measurement

Right and left hands were scanned using a Canon (LiDE 25) colour flatbed scanner. Participants were instructed to place the palm of their hand in a relaxed position with fingers evenly spaced on the glass of the scanner without applying pressure. The second and fourth fingers from two printed images were then measured by two independent experimenters. Finger lengths were measured from the basal crease to the proximal tip on the ventral surface of both left and right hand images using digital calipers (Mitutoyo Products, UK) accurate to 0.01mm. The mean value of the two experimenter measures was taken for each digit, and 2D:4D ratio calculated accordingly.

3.1.2.4 Vocal recordings and analysis

Participants were instructed to provide vocal recordings (counting slowly from 1-10) onto Olympus VN-240PC digital voice recorders at 9am (within 2 hours of waking), 12 noon and 3pm on a single day. A tolerance of +/- 10 minutes was permitted. Compliance with the procedure could be confirmed as the voice recorders recorded the time of recording, and all participants demonstrated full compliance (within -3 and +7 minutes). The files were then transferred to a PC and saved as wav files. Praat software v.3.9.2 (Boersma & Weenink, www.praat.org) was used for vocal analysis carried out as reported in section 2.1.2.

3.1.2.5 Salivary testosterone and cortisol collection and analysis

Participants were instructed to provide 3 samples of 5ml of saliva on a single day at 9am, 12 noon and 3pm using Salicaps (ImmunoBiological Laboratories, Hamburg) provided. They were asked to refrain from eating, drinking or brushing their teeth for 30 minutes prior to providing each sample, and to rinse their mouth with water 15 minutes before sample production. Participants were also asked to refrain from strenuous exercise on the testing day. All samples were frozen at -20°C until analysis in line with recommended protocol. Salivary testosterone and cortisol levels were determined using standard luminescence immunoassay kits (IBL, Hamburg) commonly used for research purposes and the in-vitro-diagnostic quantitative determination of testosterone in human saliva. Each sample at each time point was analysed in duplicate, and a mean of the two measures was used for statistical analysis.

3.1.3 Study 2a - Results

Seven individual saliva samples were excluded from statistical analysis as they were not suitable for analysis, for example, results lay outside the range of expected values for the age group concerned, or upon visual inspection blood contamination was suspected by the laboratory technician. Likewise ten individual vocal measures were excluded from statistical analyses because of technical difficulties. This explains the variation in sample size across analyses. All statistical analyses were conducted on SPSS 12.0.1 unless otherwise indicated and were two-tailed. Corrections for multiple correlations were not applied because of the exploratory nature of the investigation and because any correlations were predicted to be small.

3.1.3.1 The relationship between vocal parameters and hormone measures

The three saliva samples taken at 9am, 12 noon, and 3pm, and a daily mean value (the mean of the three samples) were correlated with measures of fundamental frequency and formant dispersion using Pearson's Product Moment correlations.

Testosterone: The daily mean value for testosterone was significantly correlated with daily mean values for fundamental frequency (r = -.512, p = .001), higher testosterone being associated with lower fundamental frequency (see figure 3c). More detailed analysis revealed a significant negative relationship between testosterone and fundamental frequency at 9am (r = -.506, p = .002) and at 3pm (r= -.360, p = .036) and a trend towards a relationship between testosterone and fundamental frequency at 12 noon (r = - .325, p = .061). There was a trend towards significance for a negative relationship between the daily mean for testosterone and daily mean values for formant dispersion (r = -.310, p = .055), with higher testosterone indicating smaller formant dispersion. More detailed analysis revealed no significant relationship between testosterone and formant dispersion at individual time points.

Cortisol: There was no relationship between the daily mean for cortisol and the daily mean for fundamental frequency although there was a significant positive relationship between these measures at 9am r = .328, p = .048, high cortisol indicating high fundamental frequency. No relationships were found between measures of cortisol and formant dispersion.

3.1.3.2 The effect of time of day on hormone and vocal measures

One-way within-subject ANOVA's with three levels (9am, 12 noon and 3pm) were carried out to examine the possible effect of time of day on measures of testosterone, fundamental frequency, and formant dispersion. Post-hoc planned comparisons (Bonferroni-corrected for multiple comparisons, $\alpha = .05$) examined differences in measures at 9am, 12 noon and 3pm.

Testosterone: There was a significant effect of time of day on circulating levels of testosterone ($F_{2,68} = 3.79$, $p = .028$), and a significant linear trend ($F_{1,34} = 4.51$, $p = .041$) with levels of testosterone decreasing throughout the day although there were no significant differences between circulating levels of testosterone at 9am, 12 noon and 3pm. Figure 3a provides the mean values at each time point.

Cortisol: There was a significant effect of time of day ($F_{(2, 74)} = 17.25$, $p <.001$) on circulating levels of cortisol and a significant linear trend ($F_{(1,37)} = 18.59$, $p < .001$. Paired samples t-tests revealed a significant difference between measures of cortisol at 9am and 12 noon $t(37) = 2.34$, $p <.001$ and between 9am and 3pm $t(38) = 2.12$, $p <.001$ but no difference between 12 noon and 3pm.

Fundamental frequency: There was a significant effect of time of day ($F_{2, 68} = 9.92$, $p <.001$) on fundamental frequency, and a significant linear trend ($F_{1,34} = 16.73$, $p < .001$) with fundamental frequency. There was a significant difference between fundamental frequency at 9am and 3pm ($p = .001$) and a trend towards significance for a difference between measures of fundamental frequency at 12 noon and 3pm ($p = .062$). Figure 3b provides the mean values at each time point.

Formant Dispersion: There was no significant effect of time of day and there were no significant differences between measures of formant dispersion at 9am, noon and 3 pm.

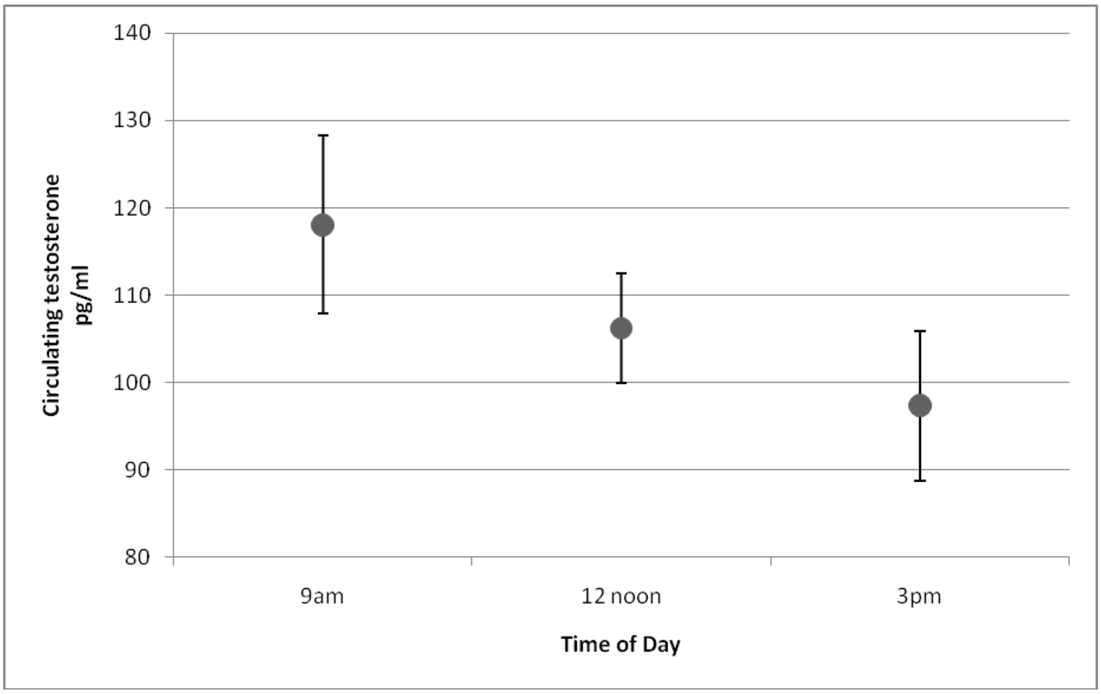


Figure 3a. Diurnal variation in testosterone

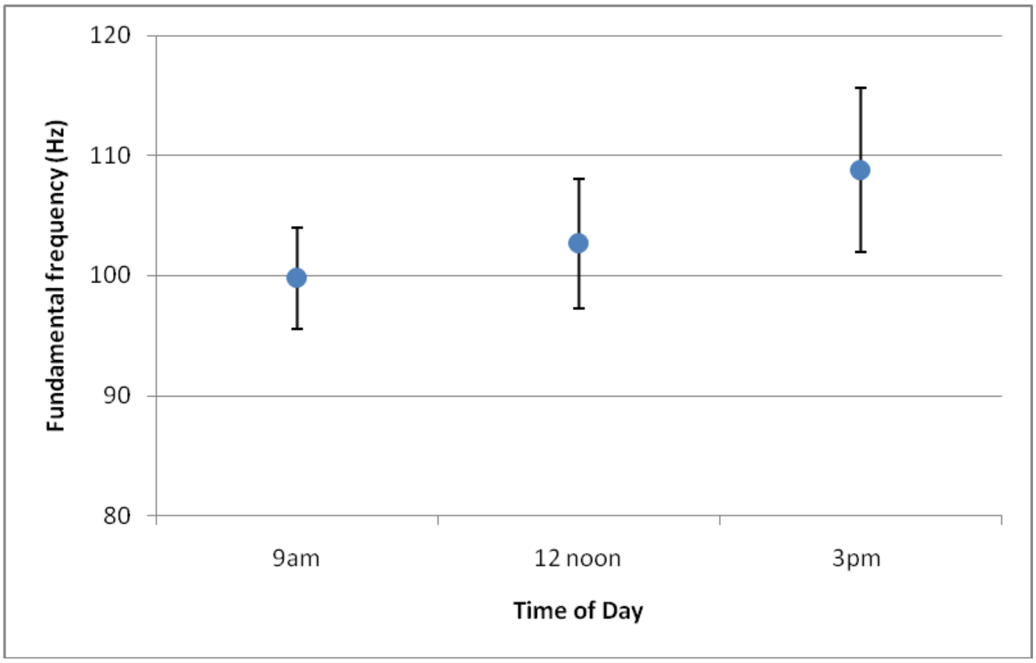


Figure 3b. Diurnal variation in fundamental frequency

3.1.3.3 The relationship between measures of the slope for testosterone and vocal frequencies.

Using Excel (Microsoft Office XP) the slope statistics were calculated for measures of testosterone, fundamental frequency and formant dispersion for each participant. Spearman rho correlations were then carried out and a trend towards significance for a negative relationship between measures of the testosterone slope and the fundamental frequency slope was observed (rho = -.331, N = 34, p = .056 (two-tailed). No other relationships approached significance.

The relationship between vocal measures and 2D:4D ratio

The concordance between the digit measurements of the two independent experimenters was calculated using Cronbach's reliability analysis which revealed high agreement in measures of the right hand (α = .996) and left hand (α = .993). The technical error of measurement (TEM) and the relative technical error of measurement (rTEM) were computed from the measures taken by the two experimenters for the 2nd and 4th digits in accordance with established protocol (Weinberg et al., 2005). For 2D measurement TEM = 0.49 and rTEM = 0.65%, for 4D measurement TEM= 0.46 and rTEM = 0.61%, indicating an acceptable level of precision (below 5%) (Weinberg et al., 2005).

Mean values for the right hand and left hand digit ratios were 0.962 (SD= 0.027) and 0.970 (SD= 0.021) respectively, comparable with reported means for a male sample in the literature. No significant relationships were observed between left or right hand 2D:4D ratio and vocal measures.

3.1.4 Study 2a - Conclusions

The current study provides supporting evidence of a significant negative relationship between daily mean values for fundamental frequency and circulating testosterone as well as individual measures at 9am and 3pm (with a trend towards significance at 12 noon); higher testosterone indicating lower fundamental frequency. Some indication of a negative relationship between the daily mean values for formant dispersion and circulating testosterone was also observed although this did not reach significance and no relationship was observed between the two measures at individual time points during the day. There was a significant effect of time of day on testosterone as expected and also a significant effect of day on fundamental frequency but not formant dispersion suggesting a novel finding for diurnal variation in fundamental frequency. Results also suggest an association between the fall in testosterone throughout the day and the rise in fundamental frequency although this relationship did not reach significance. No relationship was observed between vocal parameters and early exposure to testosterone (as measured by 2D:4D ratio).

3.2 Study 2b

3.2.1 Study 2b - Rationale

The current study attempted to replicate the novel findings of diurnal variation in fundamental frequencies observed in Study 2, as well as, the findings of a relationship between cortisol and fundamental frequency. The investigation was also extended by using a larger number of testosterone and voice measures throughout a single day and by controlling for time of waking.

3.2.2 Study 2b - Materials and methods

3.2.2.1 Participants

The sample comprised 20 healthy males aged between 18-25 years (mean = 21.37, SD = 2.17). Volunteers were recruited from the student population of Northumbria University. All were self-reported heterosexual, non-smokers with English as their first language. They reported that they were currently not suffering from any chronic diseases or hormonal abnormalities. None were currently suffering from any conditions that might affect their voice (e.g. colds, sore throats etc). They were paid £20 for their participation.

3.2.2.2 Procedure

During an initial laboratory-based training session, participants gave their written informed consent, completed a brief biographical questionnaire, and their left and right hands were scanned. They then practiced the protocol for providing saliva samples and vocal recordings, and were given the equipment and instructions necessary for them to provide both. On the day after their laboratory visit, participants were instructed to provide vocal recordings and saliva samples beginning 30min after waking, and then at six two-hourly intervals throughout the day. A tolerance of +/- 10 minutes was permitted. Record sheets and the vocal recorders ensured compliance with the procedure (within -2 and +3 minutes). Seven samples and recordings were taken from each participant in total. The methodology employed replicated the methods used in Study 1.

3.2.2.3 Vocal Recordings and analysis

This was the same as reported in section 3.1.2.4.

3.2.2.4 Salivary testosterone collection and analysis

This was the same as reported in section 3.1.2.5.

3.2.3 Study 2b - Results

Some (4/140) saliva samples were excluded from statistical analysis where individual samples were not suitable for analysis (eg. blood contamination was suspected) and likewise some (2/140) vocal samples were excluded from statistical analyses because of technical difficulties. This explains the variation in sample size across analyses. All statistical analyses were two-tailed and corrections for multiple tests were not applied because of the exploratory nature of the investigation and because any correlations were predicted to be small.

3.2.3.1 The relationship between vocal parameters and hormone measures

The 7 saliva samples, and a daily mean were correlated with measures of fundamental frequency and formant dispersion using Pearson's Product Moment correlations.

Testosterone: Daily mean values for testosterone were significantly negatively correlated with daily mean values for fundamental frequency ($r = -.498$, $p = .038$) (see figure 3d). Further analysis at each time point revealed a significant negative relationship between testosterone and fundamental frequency at 30min after waking ($r = -.623$, $p = .004$); 2.5 hours after waking ($r = -.556$, $p = .016$); 4.5 hours after waking ($r = -.609$, $p = .006$); 8.5 hours after waking ($r = -.605$, $p =.006$) and 12.5 hours after waking ($r = -.540$, $p = .017$). There were no relationships between testosterone and fundamental frequency at 6.5 and 10.5 hours after waking.

While no relationships were found between the daily mean for testosterone and formant dispersion, there was a significant negative relationship between testosterone and formant dispersion at 30min after waking ($r = -.613$, $p = .005$) and a trend towards significance at 2.5 hours after waking ($r = -.425$, $p = .079$), as well as a significant positive relationship at 10.5 hours ($r = .480$, $p = .044$). Statistical analysis comparing the difference in the coefficients at 30 minutes and 10.5 hours after waking revealed a significant difference $Z = -3.441$, $p = .0006$ (two-tailed)

Cortisol: No relationships were observed between measures of cortisol and measures of vocal frequencies.

3.2.3.2 The effect of time of day on hormone and vocal measures

One-way within-subjects ANOVA's were carried out to examine the effect of time of day on measures of circulating testosterone, cortisol, fundamental frequency and formant dispersion.

Testosterone: There was a trend towards significance for an effect of time of day on circulating levels of testosterone ($F_{6,96} = 2.07$, $p = .064$) but there was a significant linear trend ($F_{1, 16} = 8.709$, $p = .006$).

Cortisol: There was a significant effect of time of day on levels of cortisol ($F_{6,96} = 15.039$, $p < .001$) and a significant linear trend ($F_{1,16} = 29.22$, $p < .001$).

Fundamental frequency: There was no significant effect of time of day on fundamental frequency, although there was a significant linear trend ($F_{1,16} = 12.453$, $p = .003$).

Formant Dispersion: There was no significant effect of time of day on formant dispersion or any significant trend.

3.2.3.3 Study 2b - Conclusions

The current study provides further supporting evidence for a negative relationship between various measures of circulating testosterone and fundamental frequency (see figures 3c and 3d for relationships between the daily mean values for fundamental frequency and the daily mean values for circulating testosterone in both studies)

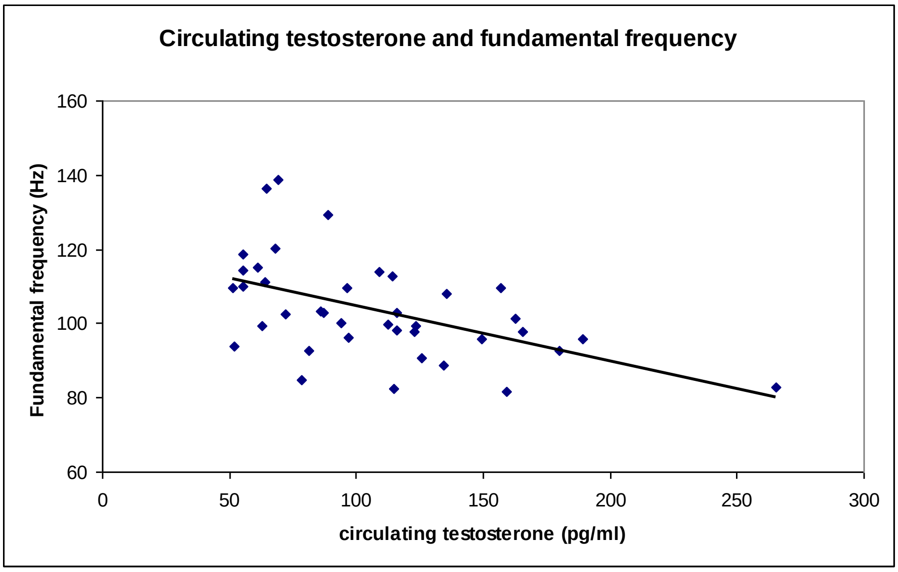


Figure 3c: Study 2a - The relationship between daily mean values (3 samples) for circulating testosterone and fundamental frequency, from a sample of 40 males (r = -.512, p=.001)

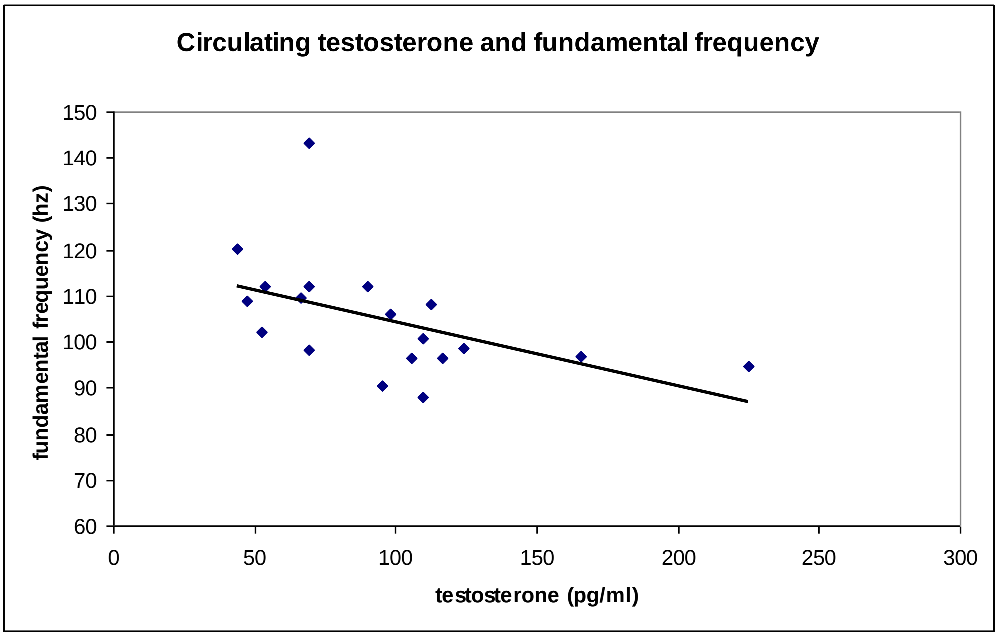


Figure 3d: Study 2b - The relationship between daily mean values (7 samples) for circulating testosterone and fundamental frequency 20 males (r19 = -.498, p=.038).

Although there was no relationship between the daily means for circulating testosterone and formant dispersion, there was evidence for such a relationship at time points through the day although the direction of the relationship changed through the day which would explain the lack of a relationship between the daily mean values. Statistical comparison of the correlation coefficents suggests that this change in direction is not just due to chance. No evidence was found for a relationship between cortisol and either vocal frequency. Diurnal variation was observed in cortisol but not testosterone or vocal frequencies.

3.3 Study 2 - Discussion

In support of previous findings (Pedersen et al., 1999; Dabbs & Mallinger, 1999) the two correlational studies reported here consistently found a negative relationship between various measures of circulating testosterone and fundamental frequency in males (see figure 3 for relationship between daily mean values for fundamental frequency and circulating testosterone in both samples). The magnitude of the relationship in the current studies was larger than observed in previous research, but is comparable to the magnitude of the relationship observed between various measures of fundamental frequency and 17 beta-estrodial in a female sample (my own unpublished data not reported in this thesis).

Results of Study 2a suggest diurnal variation in fundamental frequency that appears to reflect the diurnal variation in circulating testosterone but, as would be predicted, in the opposite direction. An association approaching significance between the fall in testosterone levels throughout the day and the rise in fundamental frequency was also observed. Such diurnal variation in fundamental frequency might explain previous contradictory findings for a relationship between circulating testosterone and fundamental frequency in past research when time of day has not been controlled. It may also explain the difference in magnitude of the relationship between the findings of the current study and previous work with correlation coefficients in Study 2a of -0.51 in the early morning and -0.36 in the afternoon. There is other evidence of temporal relationships between hormones and vocal characteristics, for example, Higgins and Saxman (1989) have shown that estrogen can influence changes in the female voice prior to menstruation and during ovulation.

Results of Study 2b did not replicate the novel finding of diurnal variation in fundamental frequency in Study 2a. However, the effect of time of day on testosterone in Study 2b was also non-significant so that whilst these findings do not therefore explicitly contradict those of Study 2a they cannot provide further clarification either. Not all males display diurnal variation in testosterone and it is therefore plausible that whilst the sample size of twenty in the second study was large enough to reveal a relationship between testosterone and vocal frequencies it was not large enough to examine the effect of time of day on either measure.

Results of Study 2a found a trend approaching significance for a negative relationship between the daily mean value for testosterone and a daily mean value for formant dispersion, with higher testosterone indicating smaller formant dispersion although no relationship between the two measures at individual time points, providing some limited support for the findings of Bruckert et al. 2006. In contrast, the results of Study 2b found no relationship between the daily means of these measures but did find a relationship between these measures at individual time-points which changed direction from negative to positive across the day. Taken together these findings suggest that the relationship between formant dispersion and testosterone may be extremely complex and deserves further investigation. Further, if investigations do not carefully account for time of day, results may be arbitrary and relatively meaningless.

Findings of the two studies study suggest that the relationship between circulating testosterone and fundamental frequency is more apparent than that between circulating testosterone and formant dispersion. This may perhaps be a reflection of the relative importance of testosterone to the changes that take place in the male larynx during puberty, with testosterone being more directly implicated in changes to the vocal folds that influence fundamental frequency than in the changes to the vocal tract that influence formant frequencies as previously discussed.

It is known that testosterone influences male vocal frequencies during puberty. Findings of the current studies and previous research suggest that testosterone continues to influence vocal frequencies during adulthood. As previously discussed, studies examining the direct effects of testosterone intervention on vocal changes in both males and females during adulthood also suggest plasticity (King et al. 2001; Akam et al., 2004, Vuorenkosi et al., 1978; Abitbol et al., 1999). Whether this relationship is causal or whether some other factor may influence both remains to be established. It is possible to speculate that perhaps fatigue may influence this relationship. Stress is another possible mediating factor but since no relationship was observed between cortisol, and vocal frequencies this is perhaps less likely.

In agreement with previous findings no relationship was found between prenatal testosterone exposure (as measured the 2D:4D ratio) and any vocal parameter measured. Although a null finding does not necessarily mean that there is no relationship, the available evidence thus far suggests that the prenatal hormone environment may not influence the adult male voice. Since sexual dimorphism of the voice to a large extent only occurs following puberty this finding is not unexpected. In the current study 2D:4D ratio was measured by two experimenters from printed scans using digital callipers. There has been some discussion in the literature about the use of scans or photocopies for 2D:4D measurement. This protocol reduces sampling times, removes the necessity for two independent researchers to be present at testing sessions and provides a permanent facsimile of the hand. Comparisons of measurements of 2D:4D from photocopies and directly from fingers show high interclass correlation coefficients (Robinson & Manning, 2000) although measures from photocopies are thought to produce lower 2D:4D values

(Manning et al., 2005). The recommendation is that the two methods should not be combined in one study or used together in comparative studies (Manning et al., 2005), which was not the case in the current study.

In conclusion, these studies support previous findings for a negative relationship between circulating levels of testosterone and adult male fundamental frequency. It also provides some limited evidence for a relationship between circulating testosterone and formant dispersion, but no evidence for a relationship between the prenatal hormone environment (as measured by 2D:4D ratio) and vocal frequencies. Novel findings in Study 2a but not replicated in Study 2b of diurnal variation in fundamental frequency that appears to reflect the diurnal variation commonly observed in testosterone, suggest that time of day should be an important consideration in future studies examining vocal frequencies. Finally, taken together, the findings of the current study support the proposition (Collins, 2000) that male vocal frequencies, especially fundamental frequency, may provide an honest signal of the speaker's hormonal quality.

Chapter Summary

The two correlational studies reported in this chapter replicated and extended previous research examining the relationship between measures of the voice and measures of circulating hormones in adult males. In support of previous work in this area a significant negative relationship between measures of circulating testosterone and

fundamental frequency, with higher levels of testosterone indicating lower fundamental frequency was consistently observed. Some limited support for a relationship between testosterone and formant dispersion was also provided although the direction of the relationship remained unclear, and results reported here suggest that such a relationship may be extremely complex. On balance evidence is lacking for a relationship between circulating cortisol and vocal frequencies. Some novel evidence for diurnal variation in fundamental frequency but not formant dispersion was found although not replicated. No evidence for a relationship between the pre-natal hormonal environment and vocal parameters. Taken together, the findings of the studies reported here support the proposition that male vocal frequencies, particularly fundamental frequency, may provide an indication of the speaker's current testosterone level and may therefore provide a signal of hormonal quality.

CHAPTER 4

The role of the male voice in intrasexual selection

Evidence from the studies reported in this thesis suggest that components of a deep male voice may be related to age, hormonal quality and also to aspects of male body shape and size. However, In order for these acoustic signals to play a role in intrasexual selection, male listeners must perceive males with deep voices as being younger, physically larger, and as dominant rivals. Further, since fundamental and formant frequencies are independent components of a deep voice in humans, the individual contribution of both to such judgements is of interest. In the first of two ratings studies, perceptions made about natural male voices by male listeners are examined. An examination of the role of male voices in intersexual selection regarding female perceptions of male voices follows in Chapter 5.

4.0 Study 3 - Rationale

Acoustic signals are known to be an important element within competitive encounters in animals. For example, Davies and Halliday (1978) found that the croak of a toad reliably informed an attacker of the size of his adversary during competition for females and, as previously mentioned, song is thought to be very important in male-male competition in birds (Kelley & Brenowitz, 2002). In non-human primates vocalisations are also thought to be important in male-male competition for mates allowing communication over long distances (Hauser, 1993; Mitani & Stuht, 1998). It is also known that in mammals, low-pitched sounds and the momentary deepening of the voice (such as growling) are used as threat signals that allow competing males to assess one other (Morton & Page, 1992). Morton (1977) suggested that low vocalisations may serve to intimidate opponents by helping the vocalizer appear to be physically larger. The size of an individual is an important determinant of the outcome of a competition if, after posturings and persuasions have been exhausted, actual combat ensues. It is therefore in the interests of an individual to make themselves appear as large as possible and exaggerate their size during the dominance displays that pre-empt fighting in order to avoid an actual fight which may be physically costly. There are many examples of animals using visual means in order to appear as large as possible during dominance displays: threatening dogs erect their hair (piloerection) and raise their ears and tails; cats arch their backs and birds extend their wings and fan their tail feathers (Ohala, 1994). These examples are referred to by Ohala as “plastic” but there are also examples of permanent or “non-plastic” size markers such as the bison’s hump, and the mane of the male lion, as well as growth of the hair around the perimeter of the face in many primates, including humans (Guthrie, 1970). Size is primarily conveyed by visual means since, in most (although not all) situations the listener is usually able to both see and hear the speaker; but it is likely that low vocalisations also play a role by adding to the impression that the speaker is large and dangerous.

The first aim of the current study was to examine whether male listeners' perceptions of voices were consistent with previous findings of relationships between aspects of the voice and age, and body shape and size. Male listeners were asked to estimate the age, body size and shape of male voices representing low and high fundamental frequency and small and large formant dispersion to assess whether perceptions of voices were consistent with actual relationships between vocal frequencies and these factors.

The second aim was to examine the role of fundamental and formant frequencies upon attributions of dominance. Of relevance is a study by Feinberg et al. (2005) experimentally manipulated human male voices speaking vowels using computer software; raising fundamental frequency by 20Hz, manipulating apparent vocal tract length by raising and lowering the entire sound spectrum and then manipulating fundamental frequency back to original values and a combined manipulation intended to create novel voices with 16 year old and 20 year old characteristics. Voices with lowered fundamental frequency were rated by females as more masculine than voices with raised fundamental frequencies. Voices with increased apparent vocal tract lengths were also rated as more masculine than voices with decreased apparent vocal tract lengths. Further, voices with the control manipulation of reconstructed original fundamental frequencies and vocal tract lengths were rated as more masculine than voices with a combined manipulation of raised fundamental frequencies and increased apparent vocal tract lengths. Another study by Puts et al (2006) examined male listeners' judgements of the dominance of male speakers by experimentally manipulating male voices. The fundamental frequency of recordings of male voices engaged in competitive vocalisations were raised and lowered one semitone using CoolEdit 2000 which also resulted in altered formant frequencies that were generally in the same direction as the fundamental frequency manipulation. Deeper voices were rated as being more 'dominant'. However, in this study fundamental and formant frequencies were simultaneously manipulated thus preventing the examination of the relative contribution of each independent component of the voice on such judgements. Some previous research has specifically examined the influence of fundamental frequency on attributions of dominance but such findings are contradictory. Aronovitch (1976) found no associations between speakers' fundamental frequency and ratings of dominance. Tusing & Dillard (2000), Scherer et al. (1973) and Scherer & Oshinsky (1977) found a significant positive relationship and Ohala (1982) found a significant negative relationship. Any relationship between fundamental frequency and dominance therefore remains equivocal, however, the relationship between body size and shape and formant frequencies suggests that formant frequencies may influence attributions of dominance, although this hypothesis has yet to be tested. The current study thus aimed to tease apart the role of fundamental and formant frequencies upon attributions of dominance.

Finally, since deep voices are thought to attract females and it would be in the interest of males to be aware of the attractiveness of male rivals, the third aim of the current study was therefore to examine male perceptions about the attractiveness of male voices to females.

4.1 Study 3 - Method and materials

4.1.1 Participants

Participants were recruited on a voluntary basis from the Northumbria University campus. Forty male participants aged between 18 and 44 (mean = 21.80, SD = 5.21) took part in the study. All participants reported that they were heterosexual, had no hearing problems, did not suffer from any chronic diseases or hormonal abnormalities or regularly take medicines, and that English was their first language.

4.1.2 Materials

Twelve vocal recordings were selected from recordings developed in Study 1 in which fifty self-reported heterosexual males had their voices recorded counting from 1-10 in their normal speaking voice. From these recordings twelve samples were chosen as stimuli for the current study representing stimuli from four groups consisting of the natural voices of males with the lowest and highest fundamental frequency and the smallest and largest formant dispersion: Low F_o (mean = 86.52, sd = 8.53) and small D_f (mean = 1543.45, sd = 29.25); low F_o (mean = 95.64, sd = 6.54) and large D_f (mean = 1733.65, sd = 31.15); high F_o (mean = 110.74, sd = 8.14) and small D_f (mean = 1504.66, sd = 118.13); high F_o (mean = 113.09, sd = 8.90) and large D_f (mean = 1767.58, sd = 11.31). Two-way ANOVA's with fundamental frequency and formant dispersion as independent factors were conducted on the two dependent variables - measures of fundamental frequency and measures of formant dispersion. Taking fundamental frequency as the dependent variable, there was a significant difference between low and high fundamental frequency groups ($F_{1,8} = 19.95$, $p <.002$), but no difference based upon formant dispersion ($F_{1,8} = .004$, $p = 0.95$). In contrast, with formant dispersion as the dependent variable, the significant difference was now between small and large formant dispersion groups ($F_{1,8} = 38.72$, $p < .0003$), with no difference between fundamental frequency groups ($F_{1,8} = 1.51$, $P = 0.254$). There were no significant interaction effects. It can therefore be concluded that the four groups of stimuli satisfied the selection criteria and differences were either present or not present on the variables as intended.

Formant dispersion was used as a single measure of formants, and short samples of counting were presented to minimise confounding variables such as accent or speech patterns, whilst allowing natural voices to be used as stimuli in order to provide ecological validity.

An in-house software program was developed so that the 12 vocal recordings could be presented in a random order on a PC with JVC noise cancelling headphones and a booklet containing 12 identical record sheets was compiled to record participants' ratings of each voice and estimates of physical size.

4.1.3 Procedure

The procedure was passed by the Northumbria University School of Psychology & Sport Sciences Ethics Committee. After providing their written consent, participants completed a brief biographical questionnaire. They then listened to twelve randomly presented recordings of male voices counting from one to ten. As each voice was heard participants were requested to rate it on a seven point Likert-type scale (1 = “not at all”, 7 = “very”) for a number of attributes and to make physical estimates about the speaker.

Six questions assessed “dominant” characteristics – Is this voice: ‘dominant’, ‘assertive’,’ forceful’, ‘threatening’, ‘masculine’, and ‘competitive’? Six questions assessed “submissive characteristics” – Is this voice ‘submissive’,’ reserved’, ‘feminine’, ‘helpful’,’ insecure’, ‘sensitive’? Two further questions assessed male perceptions of the speaker’s attractiveness to women - How successful do you think this speaker is at attracting: ‘short-term, casual female partners ‘and ‘long-term, committed female partners’? Participants were then asked to make estimates of the speaker’s physical characteristics – How tall do you think this speaker is? ‘Short’ (shorter than 5 foot 6 inches), ‘average’ (between five foot seven inches and five foot eleven) or ‘tall’ (taller than six foot). What weight do you estimate this speaker is? ‘Heavy’ (over 90kgs), ‘average’ (approximately 76 kgs) or ‘light’ (below 70 kgs). Participants were also asked to estimate the shoulder-hip ratio of the speaker from a selection of five representative drawings (ratio = 1.1, 1.2, 1.3, 1.4, 1.5) and finally participants were asked to estimate the age of the speaker (teens, 20’s, 30’s, 40’s, 50’s). Participants were able to repeat each recording as necessary while completing the record sheet. They were tested singly and received a small token payment for their participation.

4.2 Study 3 - Results

4.2.1 Estimates of age

Estimates of age were not interval level data so that chi-square statistics were carried out to examine differences in frequency. There was no significant relationship between the formant dispersion of the vocal samples and estimates of age. However, there was a significant relationship between the fundamental frequency of the speaker and estimates of their age ($\chi_2 = 16.20$, df = 4, p = .003); thus speakers with low fundamental frequency were estimated to be younger with greater frequency than those with high fundamental frequency, and speakers with high fundamental frequency were more likely to be estimated as older with greater frequency than those with low fundamental frequency (See figure 4a).

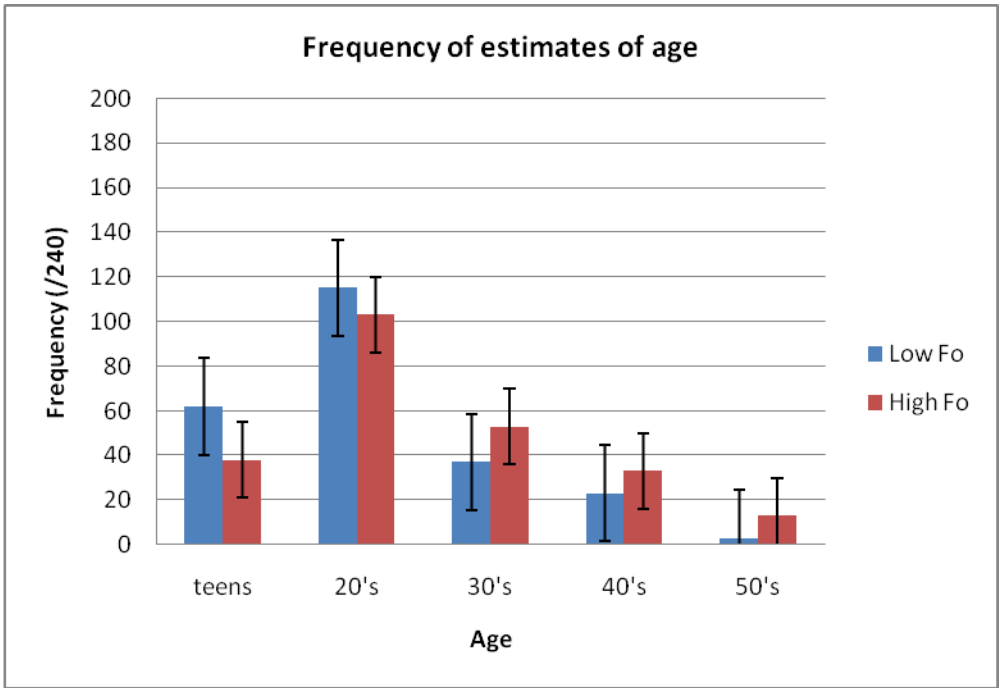


Figure 4a: Frequency of estimates of age for voices with low and high fundamental frequency.

4.2.2 Estimates of physical size

Again, estimates of physical size were not interval level data so that chi-square statistics were carried out to examine differences in frequency.

4.2.3 Formant Dispersion

Most speakers were estimated to be of average height and weight. However, estimates for the 12 voices were collapsed into two groups – small and large formant dispersion and a Goodness of Fit chi-square test was carried out to examine the differences between estimates of tall and short, and heavy and light. In line with our prediction, speakers with small formant dispersion were estimated to be *'tall'* – taller than 6 ft. ($\chi_2 = 17.34$, df = 1, $p<.001$) and *'heavy'* - over 90 kg. ($\chi_2 = 47.63$, df = 1, $p<.001$) with greater frequency than those with large formant dispersion. Conversely, speakers with high formant frequencies were estimated to be *'short'* - below 5 ft 6 ins. ($\chi_2 = 28.00$, df = 1, $p<.001$) and *'light'* – below 70 kg. with greater frequency than speakers with low formant frequencies (see figure 4b).

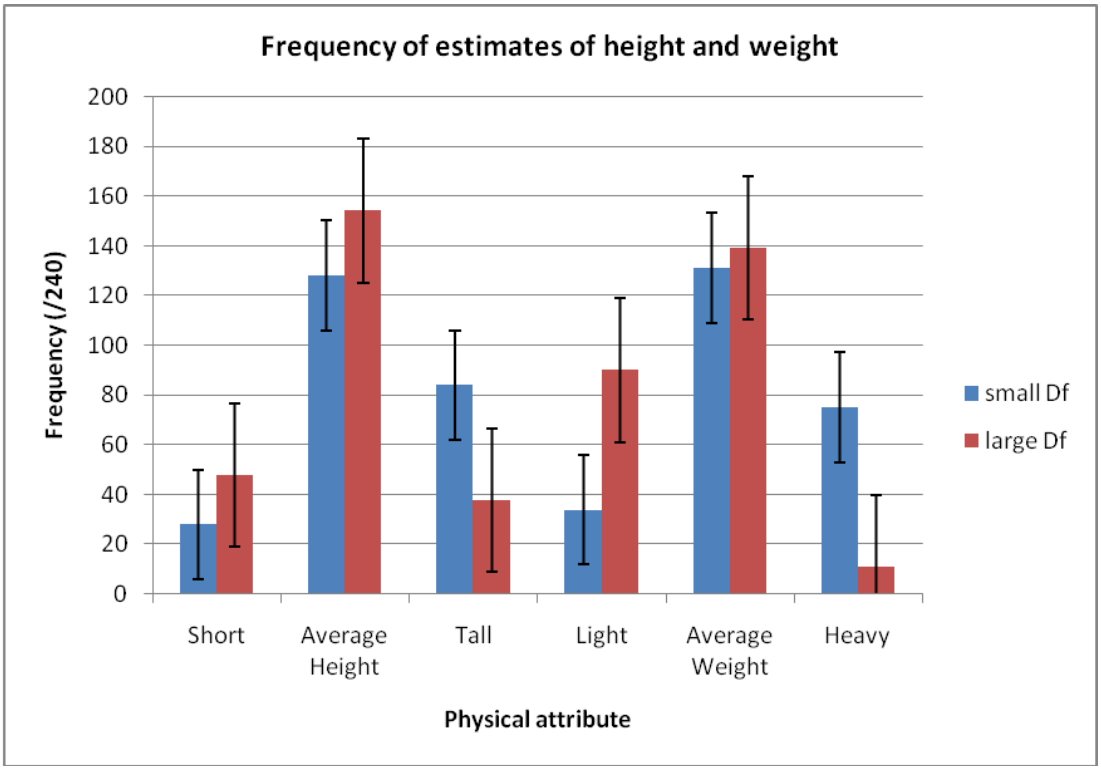


Figure 4b: Frequency of estimates of height and weight for voices with small and large formant dispersion (D_f).

Speakers with small formant dispersion were estimated to have a larger shoulder-hip ratio (ratio = 1:1.4 and 1:1.5) with greater frequency than speakers with large formant dispersion. Conversely, speakers with large formant dispersion were estimated to have a smaller shoulder-hip ratio (ratio = 1:1.1 and 1:1.2) with greater frequency than speakers with small formant dispersion (see figure 4c).

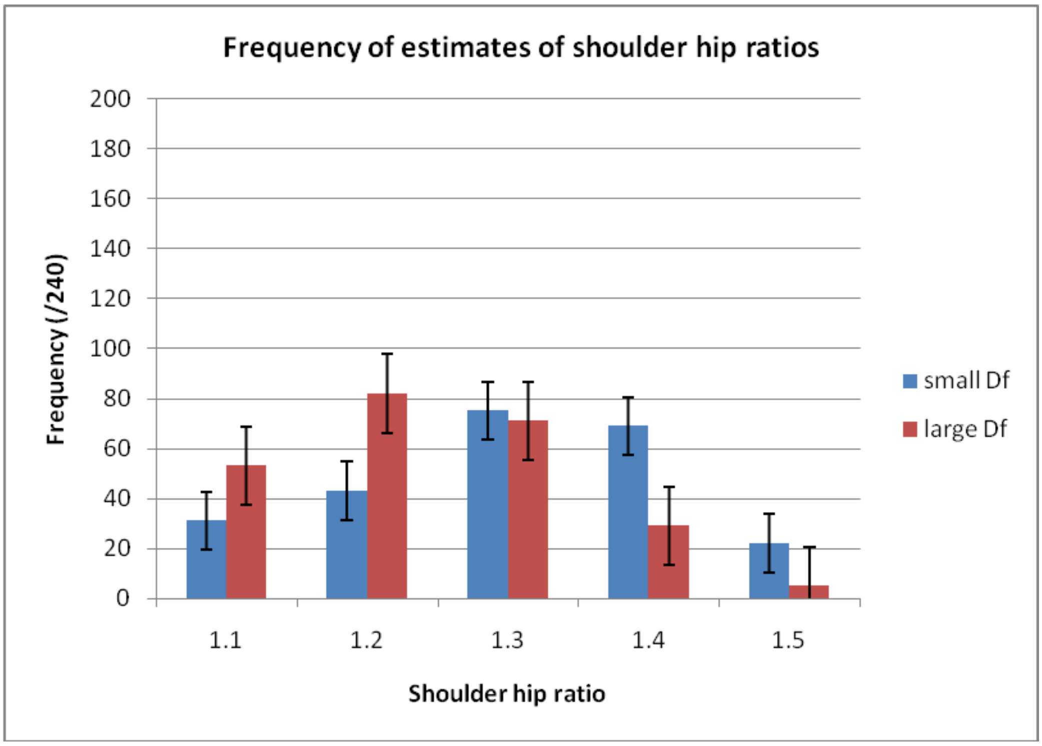


Figure 4c: Frequency of estimates of shoulder hip ratios for voices with small and large formant dispersion (D_f).

4.2.4 Fundamental frequency

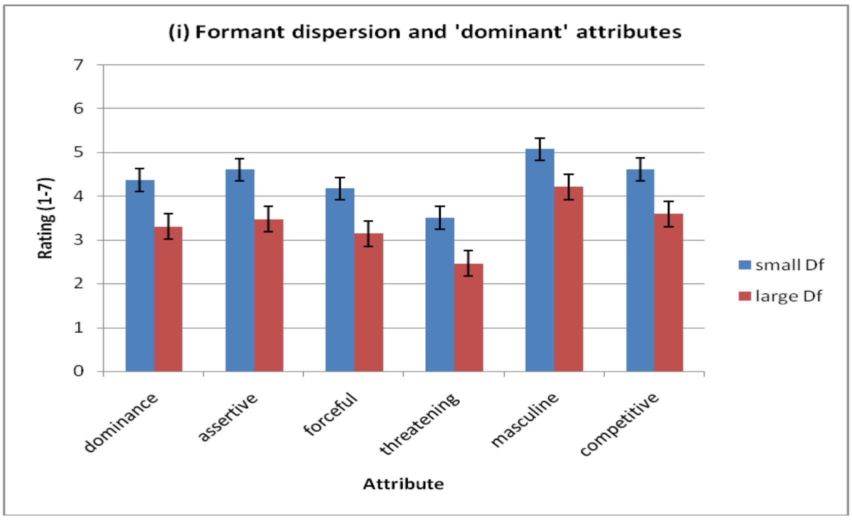
Again, most speakers were estimated to be of average height and weight. However, estimates for the 12 voices were collapsed into two groups –low and high fundamental frequency and a Goodness of Fit chi-square test was carried out to examine the differences between estimates of tall and short, and heavy and light. Speakers with high fundamental frequency were estimated to be ‘heavy’ – over 90kg ($\chi_2 = 4.88$, df = 1, p =.027) with greater frequency than those with low fundamental frequency. A multi-dimensional chi-square test was carried out to examine differences in estimates of shoulder-hip ratio between voices with low and high fundamental frequency. There was no significant relationship.

4.2.5 Ratings of dominance/submissiveness

The judge's ratings for each group of voices were averaged, and a 2-way repeated measures ANOVA (2-tailed) was carried out using SPSS software (v.12.0.1) to examine differences in male listeners ratings of male speakers in each of the four groups for a number of perceived attributes. The first factor was fundamental frequency with 2 levels (low and high). The second factor was formant dispersion also with 2 levels, (small and large). Male listeners rated the voices with small formant dispersion (low formant frequencies) as being significantly more '*dominant*', '*assertive', 'forceful', 'threatening', 'masculine'* and '*competitive*' than voices with large formant dispersion (high formant frequencies). Conversely, listeners rated the voices of males with large formant dispersion (high formant frequencies) as being significantly more *'reserved', 'feminine', 'helpful', 'insecure'* and '*sensitive'* (see Table 4a and Figure 4dii). In addition, voices with high fundamental frequency were rated as being significantly more *'helpful'* and *'sensitive'*. (see table 4a).

Attribute	**F = (1,39)**	**p ***	**Mean Rating (1-7)**	**Mean Rating (1-7)**
1st Factor - F_o			**Low F_o**	**High F_o**
Helpful	15.52	<.001	3.85 (.01)	**4.26 (.10)**
Sensitive	9.70	=.042	3.51(.09)	**3.82 (.10)**
2nd Factor - D_f			**Small D_f**	**Large D_f**
Dominant	65.35	<.001	**4.37 (.73)**	3.30 (.65)
Assertive	72.32	<.001	**4.60 (.64)**	3.47 (.60)
Forceful	73.63	<.001	**4.17 (.83)**	3.14 (.66)
Threatening	70.22	<.001	**3.50 (.90)**	2.46 (.41)
Masculine	57.22	<.001	**5.07 (.57)**	4.21 (.50)
Competitive	15.90	<.001	**4.61 (.82)**	3.59 (.43)
Reserved	34.40	<.001	3.17 (.55)	**4.03 (.30)**
Feminine	42.40	<.001	2.33(.73)	**3.15 (.72)**
Helpful	13.33	=.014	3.81 (.56)	**4.30 (.47)**
Insecure	13.10	=.014	3.07 (.41)	**3.53 (.58)**
Sensitive	50.37	<.001	3.24 (.79)	**4.09 (.59)**

Table 4a. Significant main effects of fundamental frequency (F_o) and formant dispersion (D_f) on ratings of voices for a number of perceived attributes (N=40). Means and standard deviations (in parentheses).
* a Bonferroni correction for multiple statistical tests was applied (p x14)



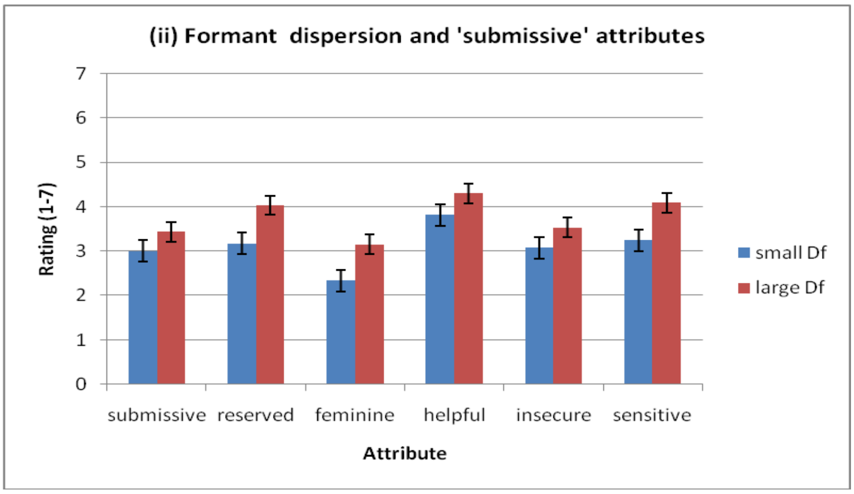
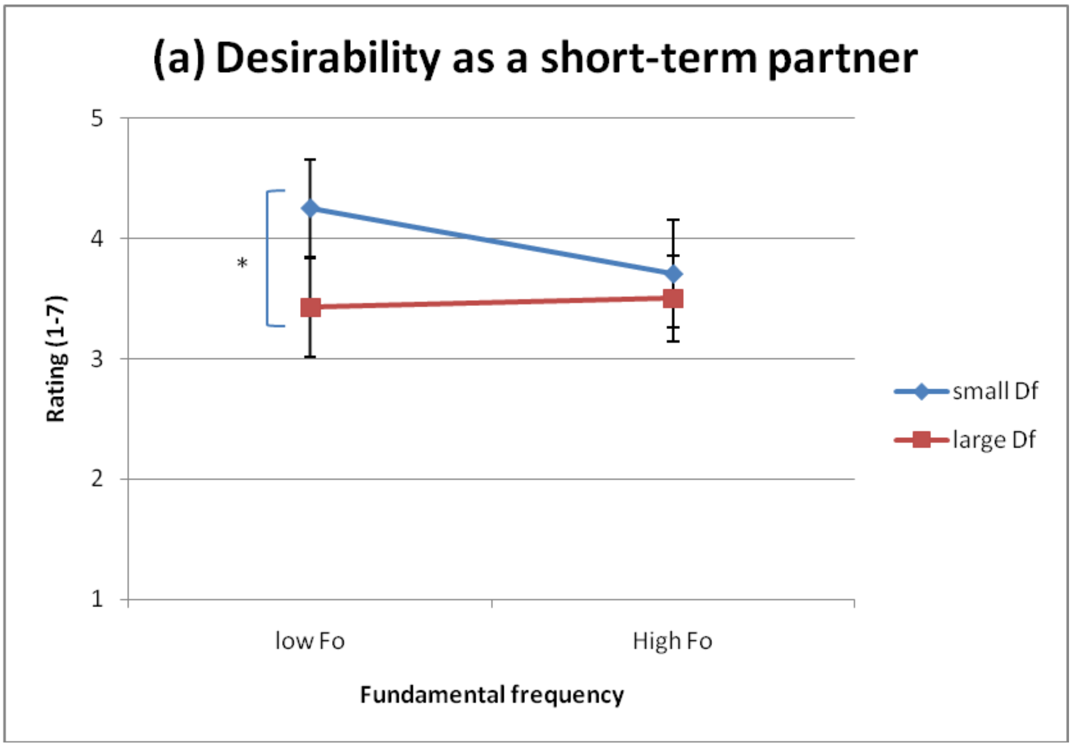


Figure 4d: Differences between ratings for voices with small and large formant dispersion for (i) dominant and (ii) submissive attributes.

No significant interactions were found for ratings of dominance and submission.

4.2.6 Ratings of desirability to females

A 2 (fundamental frequency) x 2 (formant dispersion) repeated measures ANOVA revealed a significant main effect of fundamental frequency ($F_{1,39}$ = 4.38, p = .04) and formant dispersion ($F_{1,39}$ = 18.43, p <.001) on ratings of desirability to females as a short-term partner. Voices of males with low fundamental frequency (mean = 3.84, sd = .10) were rated higher than voices with high fundamental frequency (mean = 3.60, sd = 3.60) and voices with small formant dispersion (mean = 3.98, sd = .10) were rated higher than voices with large formant dispersion (mean = 3.47, sd = .10). There was no significant main effect for fundamental frequency or formant dispersion on ratings of desirability as a long-term partner. There were however significant interactions between fundamental frequency and formant dispersion for judgements of the speakers' success at attracting both short-term ($F_{1,39}$ = 6.98, p = .01) and long-term ($F_{1,39}$ = 7.00, p = . 01) female partners . Paired samples t-tests revealed that speakers with low fundamental frequency and small formant dispersion were rated significantly higher (mean = 4.25, sd =.82) in a short term context than speakers with low fundamental frequency and large formant dispersion (mean = 3.43, sd = .83), $t_{(1,39)}$ = 4.86, p <.001), although there was no significant difference between ratings of speakers with high fundamental frequency and small (mean = 3.71, sd = .90) and large formant dispersion (mean = 3.50, sd = .72). In the long term context speakers with low fundamental frequency and small formant frequency were also rated significantly higher (mean = 4.30 ,sd = .72) than those with low fundamental frequency and large formant dispersion (mean = 3.97, sd = .79) and there was no significant difference between speakers with high fundamental frequency and small (mean = 4.22, sd = .74) and large (mean = 4.38, sd = .66) formant dispersion   Together these interactions indicate the combined influence of formant dispersion and low fundamental frequency on male listeners' ratings of male speaker's desirability to potential female mates. (see figure 4e)



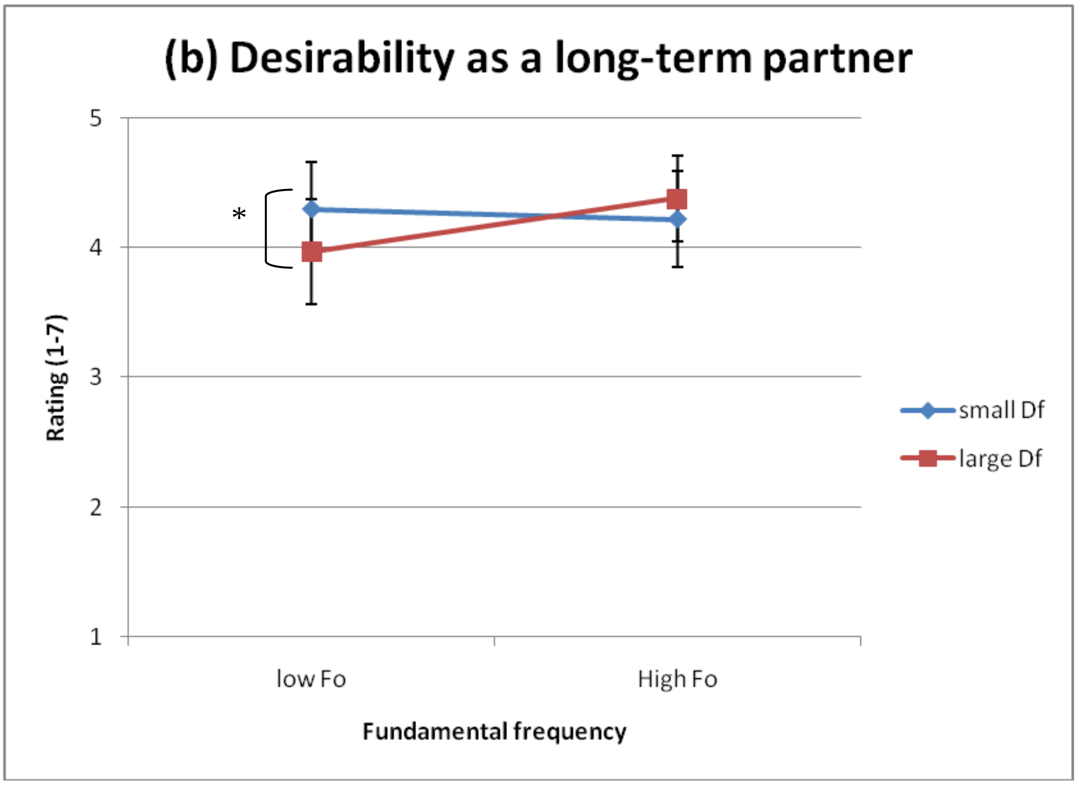


Figure 4e Interactions between formant dispersion (D_f) and fundamental frequency (F_o) for (i) ratings of desirability to females as a short-term partner and (ii) ratings of desirability to females as a long-term partner. * = significant differences.

4.3 Study 3 - Discussion

Male speakers with low formant frequencies were estimated to be physically larger – 'taller', 'heavier' and to have a 'larger' physique with significantly greater frequency than those with high formant frequencies by male listeners. They were also judged to be more dominant and less submissive. Speakers with low fundamental frequency were estimated to be younger than those with high fundamental frequency whilst speakers with high fundamental frequency were estimated to be heavier and somewhat more submissive. Finally, estimates of the success of the speaker at attracting short term female partners were influenced by both formant frequencies and fundamental frequency and there was a significant interaction between fundamental and formant frequencies for both ratings of desirability as a short term and long term partner.

Results of the first study in this thesis found that age, and aspects of body shape and size were related to fundamental and formant frequencies. The current study suggests that perceptions of male voices made by male listeners are largely consistent with these findings. Study 1 found that younger individuals had lower fundamental frequency but no relationship between formant dispersion and age. The current study found that listeners perceive post-pubertal males with low fundamental frequency to be younger than those with high fundamental frequency with greater frequency but found no relationship between formant dispersion and estimates of age.

Study 1 found no relationship between fundamental frequency and height, but that males with small formant dispersion were taller than those with large formant dispersion. Again, consistent with these findings the current study found no relationship between fundamental frequency and estimates of height but listeners perceived speakers with small formant dispersion as being taller than those with large formant dispersion with greater frequency. In Study 1 both fundamental and formant frequencies were related to weight and shoulder hip ratio, in the current study listeners perceived speakers with small formant dispersion to be heavier and to have a larger shoulder hip ratio. However, there was no relationship between fundamental frequency and perceptions of shoulder hip ratio, and a surprising result revealed that speakers with high fundamental frequency were estimated to be heavy with greater frequency.

	Fundamental frequency (Fo)	Formant Dispersion (Df)
Age	Perceptions of age were consistent with actual relationships; speakers with low Fo being younger and perceived by male listeners as such	No relationship was found between actual and perceived age.
Weight	In contradiction speakers with low Fo were heavier than those with high Fo but were perceived to be lighter.	Perceptions of weight were consistent with actual relationships; speakers with small Df being heavier and perceived by male listeners as such
Height	No relationship was found between actual height or perceptions of height and Fo.	Perceptions of height were consistent with actual relationships; speakers with small Df being taller and perceived by male listeners as such
SHR	Speakers with low Fo had a larger SHR but no relationship was observed between Fo and perceptions of SHR.	Perceptions of SHR were consistent with actual relationships; speakers with small Df having a larger SHR and perceived by male listeners as such

Table 4b. Summary table of relationships between actual and perceived age, weight, height and SHR and both fundamental frequency and formant dispersion (Inconsistencies highlighted in green text).

Taken together these findings suggest that fundamental frequency may be used as a cue by listeners to accurately assess the age of an individual, and that formant dispersion may be used as an honest indicator of height. Formant dispersion may also give some indication of body weight and body shape, although the influence of fundamental frequency on such judgements appears confusing. Although results of Study 1 suggest a relationship between fundamental frequency and weight and SHR (with heavier and larger individuals having lower fundamental frequency), the male listeners in the current study perceived speakers with high fundamental frequency as heavier, and no relationship was found between SHR and fundamental frequency (see Table 4b for a summary of relationships between actual and perceived age, weight, height and SHR and both fundamental frequency and formant dispersion). As previously mentioned, the prevalence of overweight individuals in Western society may make judgements of weight complex. It is possible due to the prevalence of obesity in western societies that weight may now be considered an indicator of ill health rather than vigour, and that this may have affected such judgements.

Results of the current study suggest that formant frequencies but not fundamental frequency indicate the dominance of the speaker to male rivals, perhaps by providing an honest signal of body size and certain aspects of body shape. A lowered larynx was, for many years, considered to be uniquely human and diagnostic of speech (Fitch & Reby, 2001). However, these authors reported that a descended larynx is not a uniquely human trait, and proposed that the original selective advantage of the descended larynx was to exaggerate the impression of size, and had nothing to do with speech. Once the larynx was lowered the increased range of formant patterns were then co-opted for speech in humans. Fitch and Reby (2001) examined the vocalizations of red deer (*Cervus elaphus*) and fallow deer (*Dama dama*).

Both of these species retract their larynges whilst roaring during the rutting season, thus elongating their vocal tracts and temporarily lowering their formant frequencies. There is a physiological limit to the extent that the larynx can be retracted, so that roaring may still provide an honest signal of body size, although the original selective advantage may have been to exaggerate it.

Fitch and Reby (2001) proposed that size exaggeration would have been highly adaptive for deer since body size and vocalisations are important in deer behaviour, influencing both aggressive and mating behaviours (Clutton-Brock & Albon 1979; McComb 1987, 1991; McElligot & Hayden 1999). Results of the current study suggest that formant frequencies play a role in human inter-male competition by providing an honest indicator of both body size and social dominance, and are in accord with Fitch's proposal that the descended larynx may be as a result of selective pressure on ancestral primates to exaggerate size within this context.

Results of the current study suggest that males appear to pay attention to both formant and fundamental frequencies when judging the success of male speakers at attracting female partners. Further research is necessary to examine the possibility that formant and fundamental frequencies are both important when females are making judgements about the attractiveness of male voices. Previous studies examining only the role of fundamental frequency in opposite-sex mate preferences may have overlooked the possible importance of formant frequencies in female preferences for deep male voices.

Some caution must be taken in drawing general conclusions from the data presented. The number of stimuli was small and a replication of the study using a wider range of stimuli is necessary before drawing conclusions that can be generalised. Also, the current study used natural stimuli in order to provide ecological validity, however, in doing so two problems arose. Firstly, using natural stimuli prevents the possibility of controlling precisely the fundamental and formant frequencies of the four groups of stimuli. In both large formant dispersion groups, fundamental frequency is also higher than the corresponding small formant dispersion group so that it is not possible to determine absolutely whether a main effect of formant dispersion is actually a result of differences in formant dispersion alone or whether there is some synergistic effect with fundamental frequency. Secondly, it is not possible to know if the natural vocal stimuli did not differ on other unmeasured acoustic properties such as jitter and shimmer, or sociolinguistic features which may affect dominance ratings. Nevertheless, the current study provides some novel evidence that male listeners use formant frequencies in the context of intrasexual selection as an acoustic signal of social dominance and body size, possibly due to a selection pressure to exaggerate size in competition with other males (Fitch & Reby 2001).

A more recent report by Puts et al. (2007) provides evidence supporting the findings of this current study. The fundamental and formant frequencies of male voices during spontaneous speech were manipulated independently but by similar perceptual amounts (just noticeable difference or JND) using computer software. Recordings of voices with low fundamental frequency or small formant dispersion were perceived as being produced by more dominant men than those with high fundamental frequency and large formant dispersion. Their results suggested however, that manipulations of formant dispersion had a greater effect than manipulations of fundamental frequency. The current study found a relationship between formant dispersion and judgements of dominance but no relationship between judgements of dominance and fundamental frequency; although fundamental frequency did influence judgements of some aspects of submissiveness, findings of the current study are therefore broadly consistent with those of Puts et al (2007). The available evidence suggests that formant frequencies may be more important than fundamental frequencies in male competition.

Chapter Summary

Acoustic signals are an important element of competitive behaviour in animals. Low vocalizations may serve to intimidate opponents by, among other things, helping the vocaliser appear physically larger. There is some evidence that deep voices in humans indicate dominance although the relative contribution of fundamental and formant frequencies to such judgments remained to a large extent unexplored. The current study recruited male listeners to estimate the age, body shape and size of male voices and to judge the

dominance/submissiveness of the speakers as well as their attractiveness to females. Speakers with low formant frequencies were rated as more dominant, less submissive and physically larger than those with high formant frequencies. Speakers with low fundamental frequency were rated as younger. Male estimates of the speaker's attractiveness to female mates suggest that both acoustic frequencies play a role in such judgements. Findings suggest that the voice, specifically the formant frequencies of the voice may play a role in intrasexual selection in humans.

CHAPTER 5

The role of the voice in intersexual selection

The fundamental and formant frequencies of the male voice may play a role in intrasexual selection in humans by indicating age, certain aspects of body size and shape, and dominance to other males. Previous research suggests that the fundamental frequency of the male voice also plays a role in intersexual selection by attracting female mates. The fourth study of this thesis explored the role of both fundamental and formant frequencies on female judgements of male voices. Further, previous findings suggest cross-modal correlations between vocal and facial attractiveness in both females and males, so that the current study also provided an opportunity to explore the relationship between visual and vocal attractiveness as well as visual and vocal dominance in human males.

5.0 Study 4 - Rationale

Considerable evidence has accumulated to suggest that fundamental frequency plays a key role in intersexual selection. Collins (2000) examined female preferences for male voices using stimuli consisting of the natural voices of 34 males (aged 18-30) uttering vowel sounds. Fifty four Dutch women (aged 18 to 30 years) listened to the stimuli, and were in high agreement that voices with low fundamental frequency were more attractive than those with higher fundamental frequency. A subsequent study in which the fundamental frequency of voices was raised and lowered by 20Hz using computer software also found that voices with lower fundamental frequencies were preferred by female listeners (Feinberg et al. 2005). Another study by Puts (2005) using stimuli consisting of unscripted male voices recorded whilst attempting to attract a female found no main effect of fundamental frequency on attractiveness ratings. However, voices with low fundamental frequency were preferred as potential partners in the fertile phase of the menstrual phase when conception risk is high and in a short-term mating context.

The first aim of the current study was to replicate the findings of previous researchers with regard to the role of fundamental frequency in intersexual selection and extend these findings by investigating whether the formant frequencies of the male voice also play a role in attracting females. Since formant dispersion is related to height (see results of Study 1) and height is linked to reproductive success in humans (Pawlowski et al, 2000), it was predicted that females would prefer the voices of males with small formant dispersion. In the Feinberg et al (2005) study although no difference in ratings of attractiveness was observed for a modest manipulation of 20Hz in formant dispersion, voices with high fundamental frequency and large formant dispersion were considered less attractive than stimuli consisting of original fundamental frequencies and formant dispersion. In a related study Feinberg et al. (2006) 'masculinised' male voices by simultaneously lowering fundamental frequency by 20Hz and lowering the formant dispersion by 50Hz. They also 'feminised' the voices by the raising the same acoustic parameters by an equivalent amount. Masculinizing male voices by manipulating both acoustic parameters increased their attractiveness to female judges and these voices were also perceived as being more dominant although the relative contribution of each acoustic parameter to such judgements was not assessed.

The second aim of this current study was to examine the relationship between acoustic and facial cues. Whilst a great deal of research has examined the importance of facial attractiveness in human attraction, the role of the voice and its acoustic components in human attraction is a relatively new field of study. One fundamental question that arises intuitively is whether facial and vocal attractiveness are related. Previous findings suggest cross-modal correlations between vocal and facial attractiveness in both females and males. For example, Collins and Missing (2003) found that women with more attractive faces also have more attractive voices as judged by men. Feinberg (2005) proposed that this correlation between faces and voices in females may reflect a common signal of information about femininity which in turn may reflect the reproductive health and development of the individual because it is positively correlated with oestrogen (Abitbol et al., 1999).

In a study by Saxton et al. (2006), female children, adolescents and adults were asked to rate the relative attractiveness of male faces and voices reciting numbers in a pair-wise comparison task. The mean attractiveness rating awarded to each male face was correlated with the mean attractiveness rating awarded to each male voice as judged by female adults and adolescents (but not children). This cross-modal concordance may be mediated by testosterone and thereby be an honest signal of immunocompetence and genetic quality (Zahavi, 1975; Folstad & Karter, 1992), alternatively, they may both correlate with dominance (Mazur & Booth, 1998); a behavioural trait also preferred by females because it implies high social status and access to resources. In their review of testosterone and dominance in men, Mazur & Booth (1998) suggested an interaction between dominance and testosterone and discussed two models that need not be mutually exclusive - a 'basal' model in which an individual's basal level of testosterone is presumed to be a fairly stable trait that predicts behaviour, and a 'reciprocal' model which suggests that challenges that elevate testosterone may in turn encourage further challenging behaviour. The second aim of the current study was therefore to replicate the findings of Saxton et al (2006) and to examine the putative relationship between visual and vocal dominance.

5.1 Study 4 – Method and materials

5.1.1 Participants

Participants were recruited on a voluntary basis from Northumbria University campus. Fifty female participants between 18 and 23 years (mean = 18.74 years, sd = 1.24) took part in the study. All participants reported that they were heterosexual, had no hearing problems, did not suffer from any chronic diseases or hormonal abnormalities and that English was their first language.

5.1.2 Materials

The twelve vocal recordings used in Study 3 examining male perceptions of male speakers were also used in the current study (see section 4.1.2 for vocal stimuli development). In addition, head-shot, colour photographs were taken of the participants against a plain background using a digital Nikon Coolpix X885 camera with a tripod. Participants were asked to remove any glasses, hats or jewellery and to adopt a neutral facial expression.

Vocal and corresponding visual stimuli were chosen to represent four groups consisting of the natural voices of males with extremes of low/high fundamental frequency and small/large formant dispersion:

Low F_o (mean = 86.52, sd = 8.53)/Small D_f (mean = 1543.45, sd = 29.25)

Low F_o (mean = 95.64, sd = 6.54)/Large D_f (mean = 1733.65, sd = 31.15)

High F_o (mean = 110.74, sd = 8.14)/Small D_f (mean = 1504.66, sd = 118.13)

High F_o (mean = 113.09, sd = 8.90)/Large D_f (mean = 1767.58, sd = 11.31).

See section 4.1.2 for statistical analyses which concluded that the four groups of stimuli satisfied the selection criteria and differences were either present or not present on the variables as intended.

An in-house software program was developed so that the twelve vocal recordings and photographs could be presented in a random order on a PC with headphones and a booklet containing twelve identical voice record sheets and twelve identical face record sheets was compiled to record participants' ratings.

5.1.3 Procedure

All participants were asked to complete a consent form before completing a brief biographical information questionnaire. Participants listened to twelve presented recordings of male voices counting from one to ten. As each voice was heard, participants were requested to rate it on a seven point Likert-type scale (1 = “not at all”, 7 = “very”) for a number of attributes on a voice record sheet. Four questions assessed attraction - How *attractive* and *sexy* is this voice? How desirable is the speaker as *a short-term, casual partner and a long-term committed partner*? These traits were chosen to obtain an overall assessment of attraction and also an assessment dependent on temporal context. Four questions assessed dominance – How *masculine, dominant, assertive* and *sensitive* is this speaker? These traits were chosen because ratings by males had previously been observed (Study 3) to be related to vocal characteristics. Participants also viewed the twelve photographs that corresponded with the vocal recordings (ie. they viewed the photographs of the individuals who had also provided the vocal recordings) and completed a face record sheet for each face identical to the voice record sheet. Participants either listened to the vocal recordings first and then viewed the photographs or viewed the photographs first and then listened to the vocal recordings. Order of presentation was counterbalanced across participants and voices and faces were randomly presented to each participant.

5.2 Study 4 - Results

5.2.1 Differences in ratings of attributes for vocal stimuli

A 2 (fundamental frequency) x 2 (formant dispersion) repeated measures ANOVA carried out using SPSS software (v.12.0.1) revealed that speakers with voices of low fundamental frequency were rated as more *desirable as a short-term partner,* as well as more *masculine* than speakers with voices with high fundamental frequency. Voices with high fundamental frequency were rated as more *sensitive* than voices with low fundamental frequency. There was no significant effect of fundamental frequency on ratings of *attractive, sexy,* and *desirability as a long-term partner*. Speakers with small formant dispersion were rated as being significantly more *masculine,* than speakers with large formant dispersion as well as more *desirable as a short term partner*. Conversely, speakers with large formant dispersion were rated as significantly more *sensitive* than those with small formant dispersion. There was no significant main effect of formant dispersion on ratings of *attractive, sexy* or *desirability as a long-term partner* (see table 5a for main effects).

	VOICES			
Perceived Attribute	**F = (1, 49)**	**p***	**Mean Rating**	**Mean Rating**
1st factor Fundamental Frequency			**Low Fo**	**High Fo**
Attractive	x	X	X	X
Sexy	x	X	X	X
Desirability short-term	8.42	=.048	3.84 (.12)	3.40 (.12)
Desirability long-term	x	X	X	X
Masculine	9.51	=.024	4.80 (.11)	4.41 (.10)
Dominant	x	X	x	X
Assertive	11.95	=.008	3.73 (.12)	3.46 (.11)
Sensitive	12.74	=.008	3.27 (.12)	3.64 (.11)
2nd factor Formant Dispersion			**Small Df**	**Large Df**
Attractive	x	X	x	X
Sexy	x	X	x	X
Desirability short-term	13.20	=.008	3.84 (.12)	3.39 (.12)
Desirability long-term	x	X	x	X
Masculine	70.84	<.001	5.10 (.10)	4.12 (.11)
Dominant	94.62	<.001	4.23 (.13)	3.12 (.10)
Assertive	11.95	=.008	3.72 (.13)	3.46 (.12)
Sensitive	32.95	<.001	3.12 (.12)	3.80 (.11)

Table 5a – Significant main effects of fundamental frequency and formant dispersion on ratings of voices and faces for a number of perceived attributes (n= 50)

*** A Bonferroni correction for multiple statistical tests was applied (p x 8)**

Two significant interactions were revealed for the ratings of *assertiveness* and *dominance*, which supersede the main effects (see table 5a) for these two attributes. There was a significant crossover interaction between fundamental frequency and formant dispersion for ratings of *assertive* $F_{1,49} = 19.58$, $p < .001$ (see figure 5a (a)). A paired samples t-test revealed that speakers with low fundamental frequency and small formant dispersion were rated significantly more assertive (mean = 4.22, sd = 1.06) than speakers with low fundamental frequency and large formant dispersion (mean = 3.23, sd 1.07), t

$_{(1,\ 49)} = 6.20$, $p < .001$. However, those with high fundamental frequency and large formant dispersion were rated higher (mean = 3.69, sd = 1.12) than speakers with high fundamental frequency and small formant dispersion (mean = 3.23, sd = 1.07), $t_{(1,49)} = -2.31$, $p = .03$. Both main effects were significant, but the interaction reported here shows that both formant dispersion and fundamental frequency are important in the judgement of assertiveness.

There was also a significant interaction between fundamental frequency and formant dispersion for ratings of *dominance* $F_{1,49} = 9.14$, $p = .032$ (see figure 5a (b)). Although there was a main effect of formant dispersion for ratings of dominance, the effect was attenuated with high fundamental frequency ($t_{(1,40)} = 9.43$, $p < .001$) compared with low fundamental frequency ($t_{(1,40)} = 3.96$, $p < .001$).

For both of these attributes the effect of one vocal frequency appears to be dependent on the value of the other. No other interactions were found.

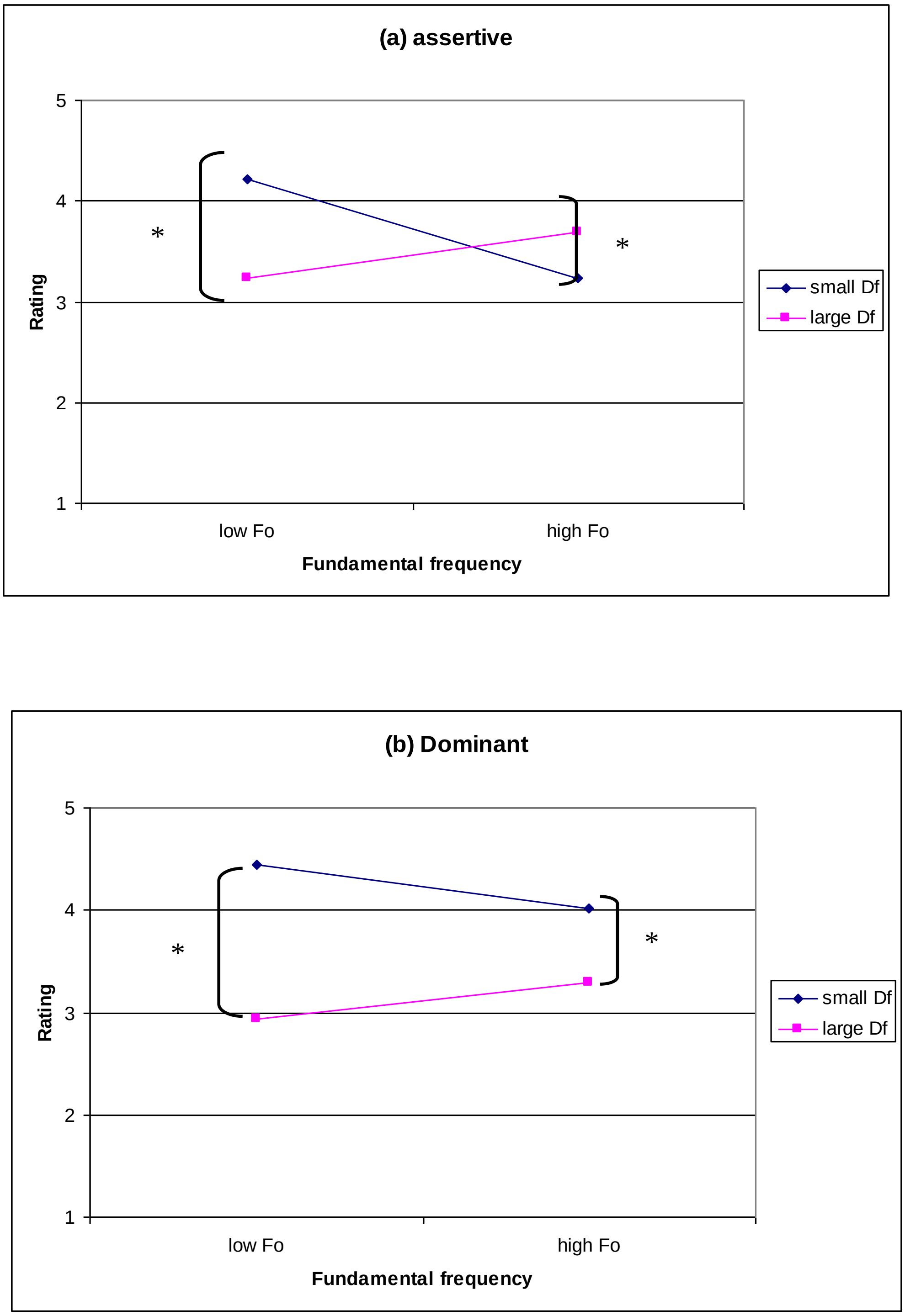


Figure 5a Interactions between fundamental frequency and formant dispersion for attributions of (a) assertiveness and (b) dominance. * = significant differences.

5.2.2 Correlations between ratings of visual and vocal stimuli

Pearson Product-Moment Correlations were carried out using SPSS software to examine relationships between ratings of voices and faces for the attributes. Ratings of voices and faces were significantly correlated for the following attributes: *attractive* ($r = .59$, $p = .04$), *desirability as a short-term partner* ($r = .66$, $p = .02$), *masculine* ($r = .69$, $p =.02$), *dominance* ($r = .83$, $p = .001$) *assertive* ($r = .62$, $p = .03$), *sensitive* ($r = .62$, $p = .03$). No significant relationship was found between ratings of voices and faces for the attributes *sexy* and *desirability as a long-term partner.* Bonferroni Corrections for multiple correlations (p x 8) removed all significant correlations except the relationship between ratings of dominance for voices and faces ($r = .83$, $p = .008$). Bonferroni is a simple but conservative approach to correcting for the occurrence of type 1 errors due to multiple statistical tests. Although there is no formal consensus as to when to use Bonferroni and it results in a substantial reduction in statistical power, many reviewers suggest their use if results could be perceived as a 'fishing expedition'.

5.3 Study 4 - Discussion

Female listeners rated the voices of males with low fundamental frequency as more *desirable as a short-term partner* than voices of males with high fundamental frequency. Voices with low fundamental frequency were also rated as more *masculine* and *assertive,* whilst voices with high fundamental frequencies were rated as more *sensitive*. Voices with small formant dispersion were also rated as more *desirable as a short-term partner*, and more *masculine, dominant* and *assertive* than voices with large formant dispersion whilst voices with large formant dispersion were rated as more *sensitive.* There was also a significant interaction between formant dispersion and fundamental frequency for the attributes *assertive* and *dominant*. Finally, there was a significant correlation between ratings of male faces and voices for *dominance* but in contradiction to previous research no relationship was observed between the *attractiveness* of male voices and faces.

With regard to questions relating to overall attraction, no differences were found between ratings of voices with low and high fundamental frequency for *attractiveness, sexiness* and *desirability as a long-term partner*. However, the voices of males with low fundamental were found to be more *desirable as short-term partners.* These results are consistent with the findings of Puts et al. (2005) who found no main effect of fundamental frequency manipulation upon attractiveness ratings although they did find that attractiveness ratings were affected by ovulatory cycle (not examined here due to the paucity of females in the opportunity sample not taking the contraceptive pill) and mating context. Voices with low fundamental frequency were preferred in a short term context as replicated in the current study. Evolutionary theory predicts that females will generally seek long term partners, willing to invest in themselves and their offspring but they do sometimes benefit by engaging in short term sexual relationships (Gangestad & Simpson, 2000) and it is predicted that in a short term context their preferences for males will be strongly influenced by physical traits that signal good genes (Gangestad & Simpson, 2000). Results of the current study are consistent with this prediction.

The pattern of results for voices with small and large formant frequencies in the current study matches the pattern observed for low and high fundamental frequencies with no differences between ratings of voices with small and large formant dispersion for *attractiveness, sexiness* and *desirability as a long-term partner* but voices of males with small formant dispersion were again found to be more *desirable as short-term partners.* These results suggest that formant frequencies as well as fundamental frequency may play a role in attracting female mates. A modest manipulation of formant dispersion (20 Hz) employed by the Feinberg et al. (2005) study might explain why no main effect of formant dispersion was observed by these authors. Although there is no doubt that a 20Hz manipulation of formant dispersion can be discerned it may not have been large enough to drive attributions of attractiveness.

With regard to questions relating to overall dominance, again, the pattern of results for fundamental frequency and formant frequencies were similar; speakers with low fundamental frequency and small formant dispersion were rated as more *masculine* and more *assertive* than those with high fundamental frequency and large formant dispersion. Voices with high fundamental frequency and large formant dispersion were rated as more *sensitive.* These results suggest that both vocal frequencies influence female judgements about such attributes although, voices with small dispersion were rated as more *dominant* than those with large formant dispersion but there was no difference in ratings of *dominance* based on fundamental frequency.

However, there was a significant interaction for the attributes of *dominance* and *assertive.* The interaction with regard to ratings of *dominance* demonstrated that the difference between large and small formant dispersion was influenced by fundamental frequency, such that the difference in ratings of dominance is greater for males with low fundamental frequency than those with high fundamental frequency. There was also a significant interaction effect for ratings of assertiveness. In this case speaker's with low fundamental frequency and small formant dispersion were rated higher in comparison to those with low fundamental frequency but large formant dispersion. On the contrary, speaker's with high fundamental frequency and large formant dispersion were rated higher in assertiveness in comparison to speaker's with high fundamental frequency and small dispersion. One possible explanation for this finding is that female listeners expect speakers with low fundamental frequency to also have small formant dispersion and that it is consistency with what is anticipated that is an important factor in determining such judgements that is important here. Another possible explanation is that either or both of the vocal frequencies must reach a threshold before being considered in such judgements.

Finally, results of the current study found some evidence of a relationship between ratings of voices and faces although all correlations regarding attractiveness judgements lost significance, after applying corrections for multiple statistical tests, apart from the correlation between ratings of the dominance of faces and voices. These results conflict with the findings of Saxton et al. (2006) and therefore require further investigation.

Chapter Summary

Previous evidence suggests that the fundamental frequency of the human male voice plays a key role in intersexual selection by attracting female mates. The results of the current study provide some support for these findings but suggest that formant frequencies may also play a role in such judgments. Finally, a preliminary examination of the relationship between judgments about voices and faces found a significant correlation between voices and faces for judgments of dominance only contradicting previous research that suggests visual and vocal attraction are related.

CHAPTER 6

The relative importance of the face and the voice upon attributions of attractiveness and dominance

Features of both the voice and the face of human males are thought to play a role in attracting female mates, and intimidating male rivals, although most previous research in the domain of evolutionary psychology has tended to examine these sensory modes in isolation. Initial findings from Study 4 reported in the previous chapter suggest that visual and vocal dominance are related, but that visual and vocal attraction are not. The primary aim of the current study therefore was to examine further the relationship between voices and faces, and to explore the relative importance of facial and vocal cues on judgments of both attractiveness and dominance.

6.0 Study 5 - Rationale

In human males, features of both the face (visual mode) and the voice (auditory mode) are thought to play a role in attracting potential female mates (intersexual selection). Features of the face and the voice may also indicate dominance, important in the context of intersexual selection, but also playing a role in intimidating male rivals (intrasexual selection). In two studies reported here the question of how cues from these two different sensory modalities relate to each other in humans, and whether there is an interaction between them is examined in the context of both attraction and dominance.

Most previous research examining the attractiveness and/or dominance of faces and voices has tended to focus on the visual and auditory modes in isolation. However, when people make judgements about others in every day life they are usually (although not always) exposed to both modalities simultaneously, so that the relative influence of facial and vocal cues to the perception of overall attractiveness and dominance and any interaction between them is ecologically important. Indeed, integration of information from the voice and face is thought to play a central role in human social interactions (Campanella & Belin, 2007). Such integration is thought to be advantageous since it may increase the reliability of information by exploiting redundancies between vocal and facial cues and it may also maximise the information by combining the non-redundant cues gathered from both modalities (Ernst & Bulthoff, 2004).

Integration of information from the face and the voice has most commonly been researched in the context of audiovisual speech perception. The combination of facial and vocal speech has been associated with both facilitation and interference effects. For example, speech becomes more intelligible when the speaker's face is visible (facilitation) (Benoit et al., 1994; Sumby & Pollack, 1954) and interference has been observed when incongruence between the face and voice has been experimentally manipulated (Campanella & Belin, 2007). Indeed, the 'McGurk effect' is a well known perceptual phenomenon in which vision alters speech perception quite dramatically. The incongruent presentation of a phoneme ("ba") and a viseme ("ga") can be strong enough to produce an illusory percept ("da") (McGurk & MacDonald, 1976). Such multimodal integration effects are not only thought to involve speech perception, but are also thought to concern the processing of affective states and the perception of identity information (Campanella & Belin, 2007). Furthermore, they are not limited to the influence of vision on audition and there are also examples of audition influencing vision (eg.Scheier et al.,1999). The majority of findings regarding cross-modal interactions have been accounted for by the 'modality appropriateness' or the 'information reliability' (Welch & Warren, 1980; Schwartz et al., 1998) hypotheses which suggest that the modality that is the most appropriate or reliable with respect to the given task is the modality that dominates perception in any given task. Other explanations include the 'directed attention' hypothesis which states that the modality to which a participants attention is directed to (automatically or through task instructions) is dominant (Welch & Warren, 1980) and the 'discontinuity hypothesis' which simply stated proposes that the modality in which the signal is discontinuous and therefore most salient is the mode that dominates (Shams et al., 2000).

When considering judgements about the attractiveness and dominance of an individual, one might intuitively predict that when both visual and vocal cues are available, that visual cues will dominate, however, several studies in the social psychology literature suggest that the relative influence of the voice and face on such attributions depends upon the type of judgement being made, and the situational context of the judgement (Zuckerman & Driver,1989).

For example, Ekman et al. (1980) carried out 3 experiments which correlated judgements made from observing single channels (face, body or speech) with multiple channel judgements (face, body and speech together; or face and speech together). In the first two experiments judges rated "honest" or "deceptive" video tapes (female participants either honestly or deceptively describing their feelings) that presented either the face only, the body only, speech only or the whole person. In the final experiment a speech with face condition was also included. Ratings on 12 scales were requested (eg. dominant-submissive, likeable- unlikeable, honest-dishonest). Generally, correlations between single channel and whole person or speech with face judgements showed that no single channel was most highly correlated with the whole person/speech with face judgements in the honest condition. However, in the deception condition, speech had the highest number of correlations with the whole person/speech with face judgements, illustrating that the situational context of the judgement being made has an impact on which single channel is most important. Zuckerman & Driver (1989) report that a consistent finding of studies investigating the relative influence of vocal and facial cues is that the voice exerts a greater influence on judgments of dominance whereas the face exerts a greater influence on judgements of dominance (DePaulo et al., 1978, Rosenthal et al, 1979, Zuckerman et al., 1982). They carried out two studies examining the effects of attractiveness of voice and physical appearance on impressions of personality. Judges rated the vocal and physical attractiveness of auditory or visual videotaped stimuli. Different judges then rated either the voice, face or face plus voice of the stimuli on a list of 10 adjectives representing 3 dimensions; dominance, achievement and likeability. Of relevance here is their finding in the first study that vocal attractiveness exerted a greater influence on dominance judgements whilst physical attractiveness exerted a greater influence on likability. These results were not replicated in Study 2, however, the authors propose that this pattern of results may have been influenced by the stimuli. In the first study the stimuli consisted of speakers expressing a strong interest in obtaining a job whereas in the second study the speakers read a standard paragraph that had no interpersonal significance.

Having examined the role of the voice in the context of human courtship and competitive behaviours in the first chapters of this thesis it is also important to examine the role of the voice within the context of other cues to attraction since whilst integration of such cues is clearly important it has been largely ignored by researchers. The two novel studies reported here therefore begin to explore the relative importance of multiple cues by investigating vocal and facial cues to attraction and dominance judgements.

6.1 Study 5a - Rationale

As previously reported, Saxton et al. (2006) found a relationship between the attractiveness of male voices and faces as judged by female adults and adolescents, however, whilst the results of Study 4 of this thesis provided some support for these findings, all correlations with regard to attractiveness judgements lost significance once corrections for multiple statistical tests were applied. Since such a relationship cannot therefore be considered robust, the current study re-examined and extended previous research by examining the relationship between male faces and voices and judgements of both attractiveness and dominance by both male and female judges. A larger number of stimuli than the preliminary investigation in Study 4 was employed and judges rated vocal stimuli, static visual stimuli and combined vocal and visual stimuli. With regard to attractiveness, it was predicted that ratings of voices and faces would be related in line with previous research (eg. Saxton et al., 2006).   In addition, the relative importance of such cues was investigated. It was predicted that visual cues would be more important than vocal cues in the context of attractiveness but that vocal cues might be more important in the context of dominance.

6.1.1 Study 5a – Methods and materials

6.1.1.1 Stimuli Development and Materials

a) Vocal Stimuli: 30 self-reported heterosexual males (age = 21.2 , SD =1.78) had their voices recorded counting from 1-10 in their normal speaking voice All voices were recorded using a PC with a Logic headset microphone onto Steinberg WaveLab 5.0 software and saved as wav files. The headset microphone ensured that all speakers were at a constant distance from the microphone (10 cm) when recording was taking place and a constant sound recording level was used.

b) Visual Stimuli: The same 30 individuals had a photograph taken of their clean shaven face and neck using a Cannon EOS 350 digital camera (Cannon

EF 70-300mm lens and Speedlite 430 EX flash) with a tripod against a black background. Lighting conditions and focal length were standardized. Hair was drawn away from the face using a hairband and volunteers were asked to remove any headwear or jewellery and to adopt a neutral facial expression. The images were saved as jpg images onto Windows XP and using Photoshop Elements 4 the saturation of each image was removed to provide black and white images which were then cropped in a standardised manner to remove any extraneous cues.

6.1.1.2 Participants

40 self-reported heterosexual males (mean age = 20.6, range = 18-25) and 40 heterosexual females (mean age = 20.7, range = 18-34) participated in the experiment giving a total of 80 judges. Volunteers were recruited from the student population of Northumbria University.

6.1.1.3 Procedure

The study was approved by the School of Psychology & Sport Sciences Ethics Committee, Northumbria University. Following informed written consent participants completed a brief biographical questionnaire.

Participants listened to 30 vocal stimuli presented in a random order using headphones to listen to the voices presented as wave files. As each voice was heard participants were requested to rate it on a seven point Likert-type scale (1= “not at all”, 7 = “very”) on 2 attributes: How attractive is this person? How dominant is this person? Questions were presented in a random order for each stimulus. Each 10 second vocal recording was followed by a 5 second gap for recording responses. Participants also viewed 30 visual stimuli presented on a laptop in a random order. Each stimulus was presented for 10 seconds followed by a 5 second gap for recording ratings identical to those presented for voices. Participants were randomly assigned to either rate voices first and then faces or rate faces first and then voices. All participants then participated in a series of tasks which formed part of another unrelated experiment but acted as a distracter task for the current study. These tasks took approximately 1 hour after which the participants rated the combined stimuli (consisting of the 30 voices and faces presented simultaneously) in a random order for 10 seconds followed by a 5 second gap for recording responses as before.

6.1.2 Study 5a - Results

6.1.2.1 Inter-rater reliability

The extent to which attractiveness and dominance ratings by judges' of each sex for each type of stimuli agreed with ratings given by judges of the same sex was examined. Ratings were converted into rank scores and concordance calculated using Kendall's coefficient of concordance. There was agreement on all judgements by judges of both sexes (see Table 6a) so ratings were combined across male and female participants for further analysis.

	Coefficient of concordance W (n = 40)		
	Voices	**Faces**	**Combined**
Females			
Attractiveness	W = .37**	W = .38**	W = .33**
Dominance	W = .28**	W = .29**	W = .25**
Males			
Attractiveness	W = .25**	W = .40**	W = .33**
Dominance	W = .20**	W = .24**	W = .18**

** p < .001

Table 6a: Agreement on attractiveness and dominance ratings of vocal, facial and combined stimuli between judges of each sex (Kendall coefficients of concordance).

6.1.2.2 Correlations between ratings by male and female judges:

The relationship between male and female ratings of voices, faces and combined stimuli was examined using Pearson Product Moment correlations. Male and female attractiveness ratings for voices only ($r = .849$, $p = < .001$), faces only ($r = .969$, $p = <.001$) and combined voices and faces ($r = .923$, $p = <.001$) were significantly correlated. Male and female dominance ratings for voices only ($r = .925$, $p = <.001$), faces only ($r = .895$, $p <.001$) and combined voices and faces ($r = .875$, $p <.001$) were also significantly correlated. Thus, male and female judges strongly agreed about which voices, faces and combined stimuli were attractive and dominant.

6.1.2.3 Bivariate correlations between ratings of attractiveness and dominance for voices only, faces only and combined voices and faces.

The relationship between ratings of both attractiveness and dominance for the facial stimuli, the vocal stimuli and the combined facial plus vocal stimuli was examined using Pearson Product Moment correlations. Bonferroni corrections for multiple statistical tests are reported here (p x 6) The pattern of relationships is illustrated in the correlation matrix in Table 2. First, no statistically significant associations were observed between vocal and visual attractiveness ratings or dominance ratings. However, a significant positive relationship was found between the dominance ratings of the vocal only stimuli and the dominance ratings of the combined vocal and facial stimuli ($r = .77$, $p < .001$), and between the dominance ratings of the face only stimuli and the dominance ratings of the combined vocal and facial stimuli ($r = .59$, $p = .006$). A significant positive relationship was also observed between the attractiveness ratings of the face only stimuli and the attractiveness ratings of the combined vocal and facial stimuli ($r = .91$, $p < .001$). No significant relationship was found between the attractiveness ratings of the voice only stimuli and the attractiveness ratings of the combined vocal and facial stimuli. Additional confirmatory analysis of the ratings by males and females separately revealed no notable change in the strength or significance of these findings (see Tables 6 b, c and d for details).

	Voice Attractive	Voice Dominant	Face Attractive	Face Dominant	Combined Attractive	Combined Dominant
Voice Attractive	1	.268 .153	-.090 .635	-.162 .392	.255 .173	.022 .907
Voice Dominant		1	-.223 .236	.110 .562	-.131 .490	.771** .000
Face Attractive			1	.182 .335	.905** .000	.089 .640
Face Dominant				1	.115 .547	.593** .001
Combined Attractive					1	.117 .537
Combined dominant						1

Table 6b: Correlations between ratings of attractiveness and dominance by both male and female judges combined for voices only, faces only and combined voices and faces. (Bonferroni corrections not applied)

	Voice Attractive	Voice Dominant	Face Attractive	Face Dominant	Combined Attractive	Combined Dominant
Voice Attractive	1	.231 .219	-.016 .934	-.123 .519	.359 .051	.046 .808
Voice Dominant		1	-.174 .359	.114 .548	-.042 .827	.807** .000
Face Attractive			1	.152 .424	.882** .000	.104 .585
Face Dominant				1	.090 .637	.553** .002
Combined Attractive					1	.144 .449
Combined dominant						1

Table 6c: Correlations between ratings of attractiveness and dominance by female judges only for voices only, faces only and combined voices and faces. (Bonferroni corrections not applied)

	Voice Attractive	Voice Dominant	Face Attractive	Face Dominant	Combined Attractive	Combined Dominant
Voice Attractive	1	.329 .076	-.159 .400	-.163 .388	.109 .566	.067 .727
Voice Dominant		1	-.267 .154	.068 .720	-.225 .232	.683** .000
Face Attractive			1	.247 .187	.900** .000	.030 .873
Face Dominant				1	.192 .308	.604** .000
Combined Attractive					1	.088 .644
Combined dominant						1

Table 6d: Correlations between ratings of attractiveness and dominance by male judges only for voices only, faces only and combined voices and faces. (Bonferroni corrections not applied)

6.1.2.4 Regression analyses

Further analysis was conducted to determine the relative importance of ratings of the face and the voice on judgments of both attractiveness and dominance. Multiple hierarchical regression analyses using the Enter method were carried out using ratings of voices only and faces only as predictor variables with ratings of voices and faces combined as the criterion variable.

a) Dominance judgments: Multiple regression analyses were carried out in which the predictor variables were entered at step one in independent analysis. Both predictor variables were significant; voice: Beta = .715, $p < .001$, face: Beta = .514, $p < .001$. In the first analysis, after controlling for ratings of voices in step one, ratings of face added significantly to the prediction F Change $_{(1,27)} = 49.03$, $p < .001$; R^2 Change = .261. In the second analysis, after controlling for ratings of faces in step one, ratings of voices added significantly to the prediction F Change $_{(1,27)}$ = 94.69, p <.001; R^2 Change = .504.

b) Attractiveness judgments*:* Again, multiple regression analyses were carried out in which the predictor variables were entered at step one in independent analysis. Both predictor variables were significant; voice: Beta = .340, $p < .001$, face: Beta = .935, $p < .001$. In the first analysis after controlling for ratings of faces in step one, ratings of voices added significantly to the prediction F Change $_{(1,27)}$ = 46.00, p <.001; R^2 Change = .115. In the second analysis after controlling for ratings of voices in step one, ratings of face only also added significantly to the prediction F Change $_{(1,27)}$ = 348.40, $p < .001$; R^2 Change = .868.

6.1.3 Study 5a - Conclusions

The current study found that judges agreed about which voices, faces and combined stimuli were attractive and dominant and that male and female judgments were highly correlated. However, contrary to what was predicted there was no relationship between the attractiveness or dominance of male voices and faces. An examination of the relative importance of vocal and visual cues to attraction and dominance using regression analyses suggested that the voice exerts a greater influence on judgments of dominance with an R^2 Change of .504 for voices in comparison to an R^2 Change of .261 for faces. However, the face exerted a greater influence on judgments of attractiveness than the voice with an R^2 change of .8.68 for faces in comparison to .115 for voices.

6.2 Study 5b - Rationale

Results of Study 5a found no relationship between the dominance and attractiveness of male voices and faces suggesting that each modality may contribute something different to overall perceptions of attractiveness and dominance. The current web-based study aimed to further explore the relative importance of the voice and face on such judgements by presenting male and female participants with stimuli that were either congruent or incongruent for the attribute being judged. This experimental design which presented faces and voices incongruent for attractiveness or dominance was chosen since it is the only way to relate perception to one modality more than the other and because, as multisensory illusions (such as the McGurk effect) illustrate, the effect of incongruent stimuli is often far greater than that of congruent stimuli.

6.2.1 Study 5b – Method and materials

6.2.1.1 Stimuli Development and Materials

A median split was performed on the attractiveness and dominance ratings for the vocal and facial stimuli used in Study 5a of this thesis. Four new sets of stimuli were created for each attribute each containing 2 subsets of 30 stimuli that were either congruent or incongruent for each attribute:

Attractiveness

Congruent: attractive faces with attractive voices

unattractive faces with unattractive voices

Incongruent:	attractive faces with unattractive voices
	unattractive faces with attractive voices
Dominance	
Congruent:	dominant faces with dominant voices
	submissive faces with submissive voices
Incongruent:	dominant faces with submissive voices
	submissive faces with dominant voices

None of the stimuli consisted of the voice and face of the same individual. The experiment was accessed through the internet and hosted by iPsychExpts.

6.2.1.2 Participants

720 participants accessed the experiment online. 411 submitted their data at the conclusion of the experiment (305 females and 111 males). A number of participants were removed from the statistical analyses because they did not meet the exclusion criteria (eg. They reported that they were homosexual). The total number of participants was therefore 272 females (mean age = 26.34, sd = 11.02) and 96 males (mean age: 24.56, sd = 7.43).

6.2.1.3 Procedure

The study was approved by the School of Psychology & Sport Sciences Ethics Committee, Northumbria University. Participants were recruited via e-mail and by web-based advertising and directed to the host site. After completing the consent screen participants completed a few brief biographical questions and were then randomly allocated to one of four conditions according to the subsets of stimuli described above so that no participant rated the same voice or face twice. In each condition 30 voices and faces were presented simultaneously. As each stimuli was presented in a random order, female participants were requested to rate the person's attractiveness on a seven point Likert-type scale (1= "not at all", 7 = "very"). Male participants followed the same procedure but were asked to make dominance ratings on an identical scale. Each stimuli was presented for 10 seconds followed by a 5 second gap for recording responses. At the end of the experiment a debrief screen explained that the stimuli had been previously rated for attractiveness/dominance and that none of the voices or faces belonged to the same individual. Participants were then invited to submit their data.

6.2.2 Study 5b - Results

6.2.2.1 Female ratings of attractiveness:

To examine differences in female listeners' ratings of the different stimuli a 2 (voice/face) x 2 (attractive/unattractive) ANOVA was carried out using SPSS software (v.15). (see Table 6e for means and standard deviations for each type of stimuli). There was a significant main effect of face on ratings $F = 15.24$, $p < .001$. No other main effects or interactions were found. The influence of the face was large (4.64 versus 4.12) whereas the effect of the voice was minimal (4.40 versus 4.38). See figure 6a for differences between female ratings of the attractiveness of congruent and incongruent stimuli.

Type of stimuli			face		
			Attractive	unattractive	
voice	attractive	N Mean s.d.	64 **4.617** 1.093	69 **4.178** 1.199	**4.3975**
	unattractive	N Mean s.d.	70 **4.681** .978	69 **4.070** 1.16	**4.3755**
			4.649	**4.124**	

Table 6e: Means and standard deviations for attractiveness ratings for each type of stimuli.

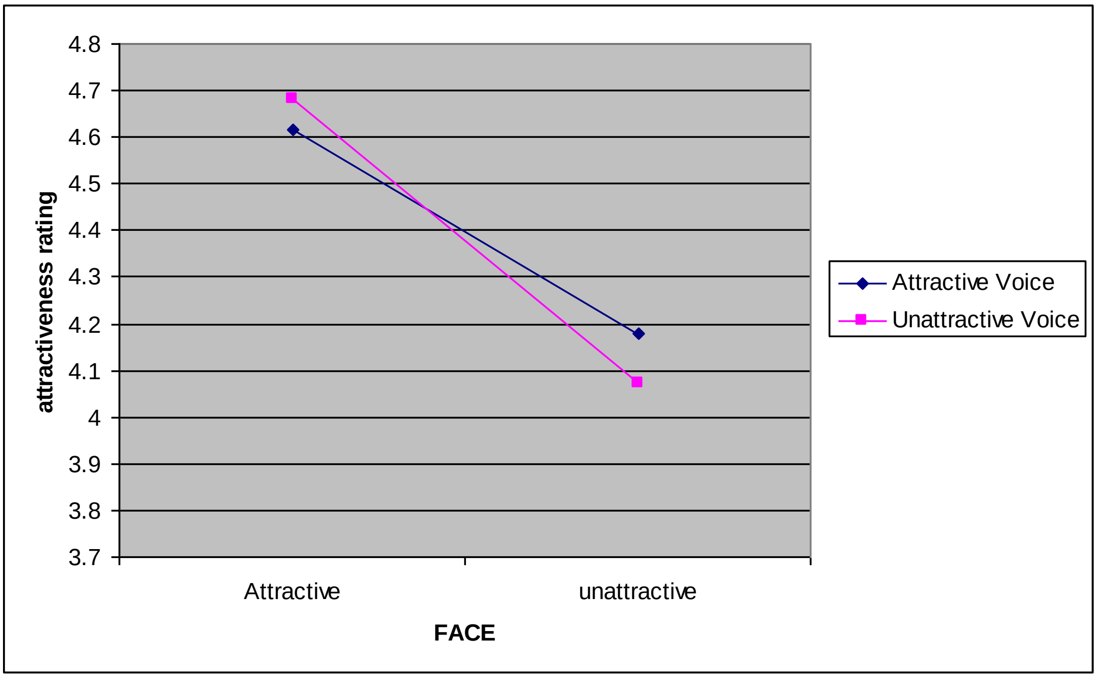


Figure 6a: Differences between female ratings of the attractiveness of congruent and incongruent stimuli

6.2.2.2. Male ratings of dominance

To examine differences in male listeners' ratings of the different stimuli, a 2 (voice/face) x 2 (dominant/submissive) ANOVA was carried out using SPSS software (v.15). (see table 6f for means and standard deviations for each type of stimuli). There was a significant main effect of voice on ratings $F = 5.13$, $p = .026$ but no significant main effect of face. However, there was a significant interaction between ratings of voice and face $F= 3.99$, $p = .042$ (see Figure 6b).

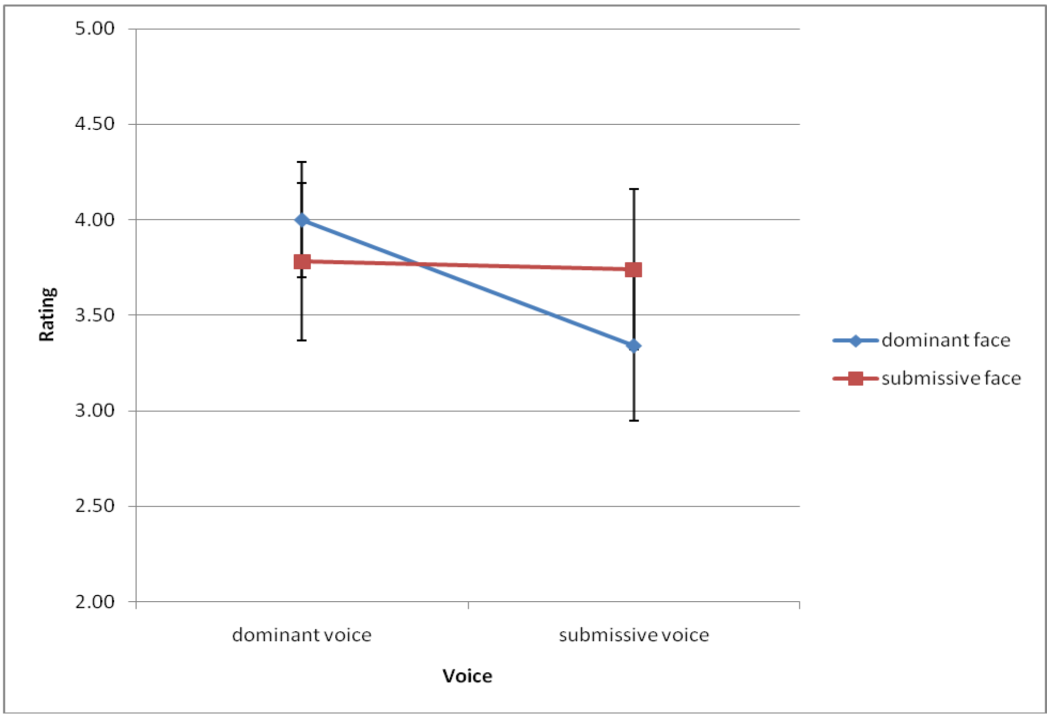


Figure 6b Interaction between dominant and submissive voices and faces.

Type of stimuli			face		
			dominant	submissive	
voice	dominant	N Mean s.d.	24 4.00 .60	24 3.78 .821	3.89
	submissive	N Mean s.d.	24 3.34 .48	24 3.74 .83	3.54
			3.67	3.76	

Table 6f: Means and standard deviations for dominance ratings for each type of stimuli.

When the face was dominant, a submissive voice had a large effect on reducing the rating, whereas when the face was submissive, there was little effect on the rating of the voice.

There was a significant difference between ratings of dominant voice/dominant face stimuli and submissive voice/dominant face stimuli ($t = 3.150$ $p = .003$). Stimuli with submissive voices but dominant faces were rated significantly lower than stimuli with dominant voices and dominant faces. There was also a trend towards a significant difference between ratings of dominant voice/submissive faces stimuli and submissive voice/dominant face stimuli ($t= 1.91$, $p = .063$). No other significant differences were observed.

An examination of the interaction and the significant differences between ratings of the four groups of stimuli show that the voice specifically influences the rating of a dominant face but not the rating of a submissive face.

6.2.3 Study 5b - Conclusions

The current study found that facial attractiveness influenced female judges perceptions of overall attractiveness of male speakers but that vocal attractiveness did not. The presentation of an unattractive face significantly reduced overall attractiveness ratings in comparison to ratings of stimuli congruent for attractiveness. Presentation of an attractive face also significantly increased overall ratings of attractiveness in comparison to ratings for stimuli congruent for unattractiveness. However in contrast, the presentation of an unattractive voice made no significant difference to overall ratings of attractiveness in comparison to ratings for stimuli congruent for attractiveness and the presentation of an attractive voice made no significant difference to ratings of overall attractiveness in comparison to ratings for stimuli congruent for unattractiveness.

In addition, results of the current study suggest that the voice but not the face influenced male judgements about the overall dominance of a speaker, specifically the voice influenced judgements of dominant faces. The presentation of a submissive voice with a dominant face reduced ratings of overall dominance compared with stimuli consisting of dominant faces and dominant voices although the presentation of a dominant voice with a submissive face did not significantly increase ratings compared to submissive voice and submissive face. This pattern of results might suggest that it is congruence between the face and the voice that is important in the context of dominance.

Results of the current study are broadly in line with the findings of Study 5a with the male voice contributing little to female perceptions of overall male attractiveness. Also in line with Study 5a of this thesis the voice influenced male perceptions of overall male dominance.

6.3 Study 5 - Discussion

Ratings by male and female judges of both attractiveness and dominance for voices, faces and the combined stimuli were highly correlated in Study 5a. This is the first study to show that male and female judgments concerning the attractiveness of male voices and faces are highly concordant, and is in line with some previous studies in the attraction literature which have found no sex differences in perceptions of female physical attractiveness (Tovée & Cornelissen, 2001; Furnham et al, 1997; Henss, 1995). It should be noted that in this study male judges were asked to judge how attractive they considered the male faces and voices to be to females, and were not asked for their own preferences. It would of course be in the interest of males to be aware of how attractive rival competitors are to females. Male and female judges also agreed about the dominance of male voices and faces

In agreement with the results of Study 4 reported in the previous chapter Study 5a found no relationship between the attractiveness of male voices and faces, contradicting previous findings from Saxton et al. (2006). The current study also found no relationship between the dominance of male voices and faces contradicting the findings of Study 4 reported in this thesis. It is possible that contradictory findings relating to the existence of a relationship between vocal and facial attractiveness in the current study may be due to possible potential confounds in the stimuli used. One potential confound is that the face stimuli consisted of cropped black and white images which were chosen in order to remove extraneous cues such as hair and eye colour. However, research has shown that skin colour alone may alter perceptions of faces (see Van den Berghe & Frost (1986) for a review of studies showing a cross cultural preference for light skin colour). The choice of black and white images may therefore have prevented a relationship between vocal and facial attractiveness being detected. However, no relationship between vocal and facial attractiveness as judged by females was also found in Study 4 which used colour rather than black and white images. Further, other researchers have also reported no relationship between vocal and facial attractiveness in males in unpublished data (Collins, 2003), and although Zuckerman et al. (1995) reported a relationship between vocal and visual attractiveness in females, they found no relationship between the attractiveness ratings of male voices and faces. Findings of such a relationship cannot therefore be considered robust. Mixed findings with regard to any relationship between vocal and facial dominance also suggest that the relationship between vocal and facial cues in such contexts may be highly complex.

If vocal and facial attractiveness and dominance are related in males, features of both may be "back-up" signals of the same quality. The back-up or redundant signal hypothesis (Møller & Pomianowski, 1993; Johnstone, 1997) suggests that different signals reflect the same aspect of quality. If, however, vocal and visual attractiveness and dominance are not related it is possible that features of the voice and the face constitute "multiple" messages. The multiple messages hypothesis (Møller & Pomianowski, 1993) suggests that multiple features signal different aspects of mate quality that are considered against one another when arriving at an evaluation to obtain a better estimate of overall mate quality than paying attention to a single ornament. These two hypotheses may be interrelated. Traits that signal different aspects of mate quality (multiple messages) can be correlated with overall quality and therefore also provide "back up" signals of an individuals overall quality (Candolin, 2003). Although no firm conclusions can be drawn from the preliminary data presented here, the results of the current study suggesting that vocal and facial attractiveness and dominance are not related would tend to support the idea that the voice and the face primarily represent multiple messages although since there is some redundant information between modalities a weak correlation might be unsurprising.

Multiple regression analysis examining the relative importance of the voice and the face on overall attractiveness ratings in Study 5a revealed that both significantly predicted overall ratings of attractiveness, although the contribution of visual cues were more important than vocal cues (accounting for 87% and 11.5% of unique variance respectively). Further, results of Study

5b suggest that facial attractiveness influenced female perceptions of overall attractiveness but that vocal attractiveness did not. In contrast, both vocal and facial cues predicted overall ratings of dominance in Study 5a but vocal cues were more important than facial cues (accounting for 50.5% and 26% of the unique variance respectively) and results of Study 5b suggest that the voice and possibly the face influenced judgements about the overall dominance of the speaker. These findings are in accordance with the findings of DePaulo et al. (1978) and Rosenthal et al. (1978).

The results of the regression analysis examining attractiveness judgments in Study 5a suggest that there may be a complex relationship between the vocal and visual modes. The different channels appear antagonistic, with the visual process actively dominating or inhibiting the auditory process. These findings are novel within this context but are in line with general findings examining human perception where inhibition commonly occurs between channels of communication (Sakagami et al, 2006 and Galinsky et al, 1990). Such findings are also in line with research examining the influence of multimodal speech perception previously discussed.

As previously mentioned, there are four hypotheses of multi-sensory integration that advocate the conditions for modality dominance. It may be that the information reliability or the modality appropriateness hypothesis might best explain the difference between the importance of the face and voice depending on the type of judgement being made; with the facial cues providing more reliable or appropriate information to the receiver in the context of attraction but vocal cues providing more reliable or appropriate cues in the context of dominance. Alternatively, it may be that attention is automatically directed in some way (indeed perhaps because the mode is more reliable or appropriate) towards one modality or the other depending on the type of judgement being made. It is, however, difficult to suggest that the discontinuity hypothesis can explain these findings since there was no difference in the structure of the stimuli.

The current study only examined the influence of vocal and static facial cues on attributions of attraction and dominance. Although this is the first study to attempt to explore the relative importance of the facial and the vocal cues to attraction and dominance within the field of evolutionary psychology, in real life observers are exposed to many more cues when making attributions about the dominance and/or attractiveness of an individual across further sensory modalities. Factors such as, body size, body shape, facial and bodily movement and odour etc. are all known to be important. Future research should examine the relative contribution of all of these factors on the attributions people make about others in the context of both inter and intra sexual selection since examining such cues in isolation may not fully account for their effects in real life particularly if the perceptual processes of different modalities inhibit one another and interact in very complex ways when making such judgments as the results of this study strongly suggest.

Chapter Summary

The two studies reported here aimed to explore the relative contribution of the face and the voice on judgements of attractiveness and dominance. Results support the suggestion that the relative importance of the voice and face to attributions people make about others depends upon the judgements being made. Unsurprisingly, the face appears to have a much greater influence on attractiveness judgements than the voice but the results of the current studies appear to show that the voice has a greater influence on judgements of dominance than the face. These findings are in line with evidence which suggests that whilst an experimental manipulation of the voice significantly affects ratings of physical dominance and sexual attractiveness the effect size is nearly 15 times greater for dominance than for attractiveness ratings (Puts, 2004).

CHAPTER 7

GENERAL DISCUSSION

7.0 Evidence for sexual selection of the human male voice

Using the five criteria for demonstrating sexual selection in communication (Snowden, 2004) (see Chapter 1) it is possible to review here the evidence for sexual selection of a deep voice in the human male:

a) Sexual dimorphism

There are only small differences in the voices of boys and girls prior to puberty (Whiteside & Hodgson, 2000), although it is possible to discriminate between them (Sachs et al, 1973) possibly due to behavioural rather than anatomical differences (Fitch & Giedd, 1999), for example, boys may protrude their lips (which has the effect of elongating the vocal tract) in order to imitate adult males (Sachs et al., 1973). However, following the major physiological changes that take place in the larynx during puberty the adult male voice is considerably deeper than the adult female voice and listeners are easily able to distinguish between them (Bennett & Montero-Diaz, 1982; Childers & Wu, 1991; Coleman, 1976). The voice is therefore sexually dimorphic but this alone is not a sufficient condition for sexual selection.

b) Variation in the signal between same-sex conspecifics

The deepest male voice consists of both low fundamental frequency and low formant frequencies. Both acoustic frequencies display within sex variation that is easily perceived by same sex and opposite sex listeners with a range of 85-155Hz reported for fundamental frequency (Baken, 1987); and ranges of 150-850Hz, 500-2500Hz, 1500-3500Hz and 2500-4800Hz for the first four formants respectively (Benade, 1990).

c) and d) Discrimination and expression of preference or avoidance in the context of mating

(i) Attracting female mates

Considerable evidence has accumulated to suggest that low fundamental frequency plays a key role in intersexual selection by attracting potential female mates (Collins, 2000). Such preferences appear to be influenced by both menstrual cycle (Feinberg et al., 2006; Puts, 2005) and by mating context (Puts, 2005). In line with the findings of Puts (2005) Study 4 of this thesis found no difference in female ratings of attractiveness for voices with low and high fundamental frequency but did find that females preferred the voices of males with low fundamental frequency as short-term partners when it is predicted that female preferences for males will be strongly influenced by physical traits that signal good genes (Gangestad & Simpson, 2000). Collins (2000) proposed that the fundamental frequency of the male voice provides a signal of hormonal quality, heritable fitness and immunocompetence to potential female mates since fundamental frequency is androgen dependent.

With regard to formant frequencies, previous findings (Feinberg et al., 2005) found no difference in attractiveness ratings for an experimental manipulation of formant dispersion although voices with both high fundamental frequency and large formant dispersion were less attractive than stimuli before manipulation. Collins (2000) also found no relationship between formants and attractiveness ratings. However, results of Study 4 of this thesis found that voices with small formant dispersion were preferred by female judges as short-term partners, suggesting that formant frequencies in addition to fundamental frequencies may play a role in attracting potential female mates. Conflicting results here may have been due to the modest manipulation of apparent vocal tract length employed in the Feinberg study (2005) and the measurement of formant frequencies by Collins (2000). The finding that formant dispersion influences attractiveness judgements by females is in line with what would be predicted since formant dispersion is thought to be an accurate cue to height and height is positively linked to reproductive success in males (Pawlowski et al., 2000). In agreement with the findings of Gonzalez (2004) the results of Study 1 of this thesis (Evans et al., 2006), found a significant negative relationship between height and formant dispersion in adult males; taller individuals had lower formant frequencies. No similar relationship was observed between height and fundamental frequency. Of relevance here (although the perceptions of females were not examined) are the results of Study 3 that suggest male listeners also perceive speakers with small formant dispersion as taller than those with large formant dispersion. Feinberg et al. (2005) did find that taller, heavier women listeners preferred male voices with increased apparent vocal tract length suggesting an assortative preference.

(ii) Intimidating male rivals

There is growing evidence that a deep voice in the human male also plays a role in intrasexual selection by intimidating other males. In a study in which human male voices were experimentally manipulated using computer software (Feinberg et al., 2005) female listeners perceived ‘masculinized’ voices as more dominant. In another study by Puts et al. (2006) which examined male listeners’ judgements of the dominance of male speakers by experimentally manipulating male voices. Deeper voices were also rated as being more ‘dominant’. However, in both of these studies fundamental and formant frequencies were simultaneously manipulated thus preventing the examination of the relative contribution of each independent component of the voice on such judgements.

Results of Study 3 of this thesis found that male speakers with small formant dispersion were rated as more dominant by male listeners and results of Study 4 found that female listeners concurred, although no difference was observed between male ratings based on fundamental frequency which is somewhat surprising. However, a subsequent study by Puts et al. (2007) found voices with both low fundamental frequency and low formant frequencies to independently be perceived as more dominant, however, formant dispersion appeared to have a greater effect on dominance ratings than fundamental frequency which may explain this finding. Since the stimuli used in the Puts et al. (2007) study consisted of unscripted male voices speaking to a competitor and the studies reported in this thesis used neutral stimuli it may be that context is crucially important here and requires further investigation. Whilst the fundamental frequency of the normal speaking voice may not provide a permanent signal of dominance temporal modulation of vocal pitch depending on circumstances may be used to advertise affect. Many animals are known to momentarily lower the pitch of their signal to indicate dominance and this may be the case in human males.

e) Outcome of preference (or avoidance) must relate to reproductive success

Although not examined in this research programme there is some emerging evidence that the voice is linked to differential reproductive success. A study by Hughes et al. (2004) suggested a relationship between the voice and sexual behaviour. They found associations between vocal attractiveness ratings and self-reported sexual behaviour. Males (and females) whose voices were rated as attractive reported having sex at an earlier age, had more sexual partners, more extra-pair copulation partners and more sexual partners that were involved in a relationship with another person. Furthermore, a recent study by Apicella et al. (2007) has linked fundamental frequency directly with reproductive success. In a study examining the reproductive success of an evolutionary relevant population of hunter gatherers fundamental frequency was found to predict reproductive success and number of children in men but not women suggesting that a female preference for males with low fundamental frequency translates to an actual reproductive advantage. Since formant dispersion is related to height in adult males (Gonzalez, 2004; Evans et al., 2006) and there is some evidence that taller males have higher reproductive success than shorter males (Pawlowski et al., 2000; Mueller & Mazur, 2001) there may also be a link between formant dispersion and reproductive success through its association with height. Further research is necessary to examine a direct link. There is also some evidence that the voice has a heritable component. Debruyne et al. (2002) found that the fundamental frequency of monozygotic twins is more similar than that of same-sex dizygotic twins and structural similarity on a genetic basis is reported for anatomical features such as the volume and morphology of the larynx and the vocal tract (eg. Sataloff, 1995)

To review, the voice of the human male is a sexually dimorphic trait that also displays within-sex variability that can be easily perceived by others. Evidence suggests that females display a preference for males with deep voices when considering potential short-term partners and there is growing evidence that deep voices also intimidate other males by indicating the dominance of the speaker. There is also recent evidence to suggest that males with deep voices enjoy greater reproductive success.

7.1 Multiple messages

Many sexual displays are examples of multicomponent signalling (Rowe, 1999) with exaggeration of several distinct signals even within a given modality. The deepest voice consists of both low fundamental frequency and low formant frequencies which are independent of one another. One of the aims of this thesis was to examine the relative contribution of these two distinct acoustic parameters, further, this research programme also aimed to examine the voice in relation to other cues to attraction, specifically facial cues since examining the voice in isolation may not account for effects in real life.

7.1.1 Multiple signals within the auditory modality

According to the Source-Filter Theory of Speech Production (Fant, 1960) fundamental and formant frequencies are independent of one another. As would therefore be predicted, statistical analysis throughout this research programme has found no significant relationship between fundamental and formant frequencies in several samples of adult male voices. Fundamental frequencies are determined by the vibration of the vocal folds and formants are determined by the size and shape of the vocal tract. Simultaneous but independent physiological changes during puberty result in lower fundamental frequency and lower formant frequencies in adult males. Further, recent neuroimaging research suggests that different cortical areas may also be responsible for their perception (Hall et al., 2003, Lattner et al., 2005; Zatorre et al., 2002).

Several lines of evidence suggest that whilst these acoustic parameters provide some redundant information they may also contain non-redundant information too.

a) Hormonal quality

No relationship between fundamental frequency and prenatal testosterone (as measured by the putative marker 2D/4D) was observed in Study 1 of this thesis consistent with the findings of Putz et al. (2004) and any such relationship therefore remains equivocal. However, fundamental frequency is negatively related to male pubertal testosterone (Harries et al., 1997) and to adult circulating testosterone levels (Evans et al., 2008; Pedersen et al., 1999 and Dabbs & Mallinger, 1999). A small number of studies have previously investigated the relationship between circulating testosterone and fundamental frequency although the findings were mixed and there were also some methodological issues. Results of Study 2 of this thesis published in Evans et al. (2008) suggest that there is indeed a consistent negative relationship between testosterone and fundamental frequency that may in fact be larger than previously reported. Results of Study 2a also suggest that there may be diurnal variation in fundamental frequency (as commonly observed in testosterone levels) which may explain the difference in magnitude between the study reported here and previous findings.

Results of Study 2a but not 2b of this thesis provide some limited support for the findings of Bruckert et al. (2006) for a weak negative correlation between circulating testosterone and formant dispersion. However, on balance the evidence suggests that formant dispersion is not a reliable or accurate indicator of male hormonal quality and that fundamental frequency and not formant dispersion provides an honest signal of hormonal quality in males.

b) Body size

In agreement with the findings of Sachs et al. (1972), Gonzalez (2004) and Bruckert et al. (2006) the results of Study 1 of this thesis found a significant negative relationship between height and formant dispersion in adult males;

taller individuals had lower formant frequencies. This correlation may be explained by the fact that vocal tract length is a determinant of formant frequencies and that vocal tract length in turn is correlated with height in humans (Fitch & Giedd, 1999).

Results of Study 1 of this thesis also found a significant negative relationship between weight and formant dispersion; individuals with smaller formant dispersion being heavier in agreement with the findings of Rendall et al., 2005). Since height is positively correlated with weight (Kunzel, 1989) such a finding is in line with what would be predicted.

Both Gonzalez (2004) and the results of Study 1 of this thesis found a weaker relationship between body size and formant frequencies than Fitch (1997) reported in rhesus macaques. One possible explanation for this finding is that the secondary descent of the larynx in human males disassociates vocal tract length from skeletal size. Gonzalez (2004) found a stronger relationship between formant frequencies and body size in human females than human males supporting this proposal.

Speakers with small formant dispersion were perceived by male listeners to be taller and heavier with greater frequency than those with large formant frequencies. Interestingly, although female perceptions were not examined within this thesis, van Dommlen and Moxness (1995) found that the ability to estimate the height and weight of adult male speakers was confined to male listeners (the estimates in this study were based on speech rate although listeners thought they were basing their judgment on the frequency of the voice).

No relationship was observed in Study 1 of this thesis between height and fundamental frequency in adult males, consistent with the findings of Collins (2000), Kunzel (1989), Lass and Brown (1978), Randall et al. (2005) and van Dommelen and Moxness (1995). Although it should be noted that fundamental frequency is negatively related to height as a function of age in pre-pubertal (Huber et al., 1999) and adolescent (Hollien et al, 1994) males. Surprisingly, a significant negative relationship was found between weight and fundamental frequency but only after age was controlled for. Other researchers have not commonly observed such a relationship (Collins, 2000; van Dommelen & Moxness, 1995). As previously mentioned, the prevalence of overweight individuals in Western society may make the examination of the relationship between weight and other variables difficult. Confusingly, the results of Study 3 suggested that male listeners perceived the opposite; speakers with high fundamental frequencies were rated as heavier than those with low fundamental frequencies. Findings that listeners incorrectly use fundamental frequency as a cue to body size within sex are not uncommon perhaps because fundamental frequency does show a reliable negative correlation with body size across sex and age since fundamental frequency is higher in children and females and lower in males. The balance of evidence thus far does not indicate that fundamental frequency can be considered an accurate indicator of the body size of an individual although it is possible it may have done so in our evolutionary ancestors.

As noted by Fitch (1997), the human vocal tract is constrained by the bones of the skull, and skull size is closely associated with overall body size; vocal tract length and formant dispersion are therefore less free to vary independently from body size than the larynx and are therefore more likely to provide a robust cue to body size than the larynx and fundamental frequency. Formant dispersion appears to provide an accurate indicator of height (Evans et al., 2006 and Rendall et al., 2005; Sachs et al., 1972) and weight (Evans et al., 2006). Fitch (1997) suggested that perceptual mechanisms for judging size information may have provided a pre-adaptation for vocal tract normalisation which is a critical aspect of speech perception whereby the sounds from different sized speakers are 'normalised', allowing a listener to recognise the vowels of speakers of different sizes as the same percept (Nearey, 1978; Lieberman, 1984).

Various aspects of body shape were found to be associated with acoustic properties in Study 1. Fundamental frequency was associated with shoulder and chest circumferences and shoulder hip ratio. Formant dispersion was related to neck, shoulder, chest and waist circumferences as well as shoulder hip ratio. With regard to perceptions male listeners make about the shoulder hip ratio of male speakers, the results of Study 3 found that male listeners rated speakers with small formant dispersion as having a larger shoulder hip ratio but again the findings with regard to fundamental frequencies were inconsistent and no difference in ratings was observed based on the fundamental frequency of the speaker. The association between fundamental frequency and upper body shape is unsurprising since both are determined by testosterone at puberty. Women are known to prefer men whose torso has an inverted triangle shape (a narrow waist with broad shoulders and chest). Less clear is the explanation for the association between formant dispersion and upper body shape although pubertal testosterone may also play a role here too.

c) Age

Previous studies examining perceptions of age based on the voice have often found correlations between actual and perceived age (Shipp & Hollien, 1969; Ryan & Burk, 1974; Hartman, 1979; Neiman & Applegate, 1990). Results of Study 1 of this thesis examining the relationship between acoustic parameters and age in a sample of males aged between 18-66 years found that age was related to fundamental frequency with young post-pubertal adult males having lower fundamental frequency than older males. No such relationship was observed between formant dispersion and age. Results of Study 3 examining male listeners' perceptions of age in which males with low fundamental frequency were estimated to be younger with greater frequency than those with high fundamental frequency were consistent with these findings. Collins (2000) and Biemans et al. (1995) also found that perceptions of the age of male speakers were based on fundamental frequency although Collins (2000) found that males with low fundamental frequency were estimated to be older than those with high fundamental frequency in a sample of males between 18 and 30 years of age.

It is possible that the inconsistency with regard to the direction of these estimates may be due to the different age range of the speakers in the two samples. The results reported in this thesis are contradictory to those of Bruckert et al. 2006 in which actual and estimated age was related to formant frequencies but not fundamental frequency. It remains unclear therefore whether fundamental frequency or formant frequencies or indeed both acoustic frequencies provide reliable indicators for age discrimination in post-pubertal males. However, Smith and Patterson (2005) examined the ability of listeners to judge size, sex and age from vowels manipulated to represent people with a wide range of fundamental frequency and vocal tract lengths from small child to giant. They also included many vowels way beyond normal range. The results for the sex and age categorization showed that judgements of speaker age and sex within the normal range were influenced about equally by fundamental frequency and vocal tract length. Both fundamental and formant frequencies are also reliable indicators for gender discrimination (Childers & Wu, 1991) suggesting that considerable redundant information concerning both age and gender are contained within the two vocal parameters so that either may be sufficient for age and gender recognition.

To review, fundamental and formant frequencies are independent of one another and the available evidence suggests that whilst they do provide some redundant information such as age, gender and possible body shape they may also provide different signals; with fundamental frequency indicating the hormonal quality of an individual and formant frequencies indicating body size. See Figure 7a for a summary.

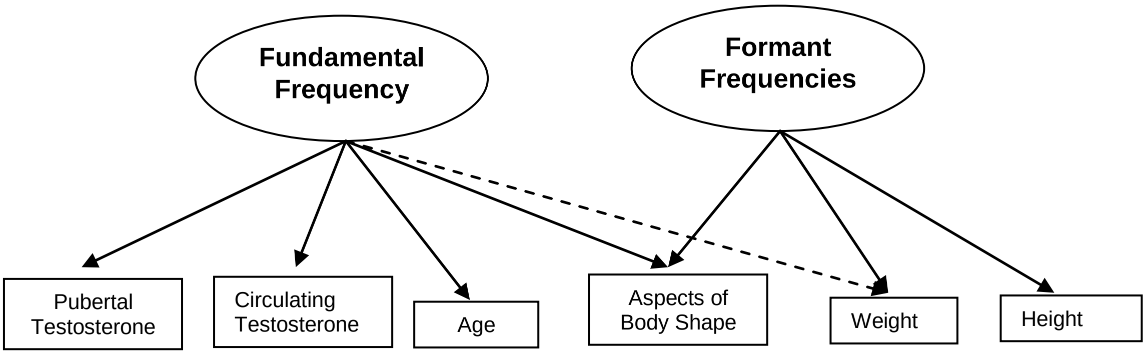


Figure 7a - Summary of relationships between vocal frequencies and measures of testosterone, age, body shape and size.

These findings are consistent with the multiple messages hypothesis (Møller & Pomiankowski, 1993, 1993; Johnstone, 1997) suggesting that different signals provide different information. However, It is possible to further speculate, in line with the multiple receivers hypothesis (Butcher & Rohwer, 1988; Andersson, 1994; Savalli, 1995) that the two components of a deep voice, formant frequencies and fundamental frequency, may have evolved under separate selection pressures by different receivers, with low fundamental frequency selected by females and low formant frequencies selected for by male rivals.

One limitation of this thesis is that it has not investigated female voices, indeed, most research in this field has tended to focus on male voices. However, such research may shed light on the selection pressures upon our ancestral relatives. One study examining men's perceptions of female voices found that women with high fundamental frequencies were considered more attractive than those with low voices (Collins & Missing, 2003). The vocal folds are affected by the influence of oestrogen and progesterone at puberty (Jenkins, 1988) and there is some evidence that female fundamental frequency continues to relate positively to estrogen in adult females (my own unpublished data) which itself is positively linked to reproductive health and development (see Alonso & Rosenfield, 2002 for a review); so that high fundamental frequency may indicate hormonal quality in females in much the same way that the relationship between high testosterone and low fundamental frequency is thought to indicate hormonal quality and immunocompetence in males. Sex differences such as this are often created and maintained by disruptive selection (selection against the mean of a trait so that a bimodal distribution is established - Trivers, 1985). It is possible therefore that there was selection pressure against androgeny in our evolutionary past that drove the sexual dimorphism of fundamental frequency in the human voice.

Whilst the same selection pressure against androgeny for fundamental frequency may explain the sexual dimorphism of formant frequencies it is a less likely explanation. It is possible that the larynx of both ancestral males and females descended but that females subsequently lost this developmental event. This explanation is perhaps unlikely if the ontogeny of the human voice and the absence of a descended larynx in non human primates is considered (Puts, 2007). I propose a more parsimonious hypothesis; that the secondary descent of the larynx which lengthens the vocal tract in males and creates lower formant frequencies evolved separately from the mechanism that influences fundamental frequency under directional selection in order for males to exaggerate the appearance of size in the context of intrasexual selection (Fitch & Giedd, 1999) (see figure 7b).

It is clear that findings of relationships between both acoustic parameters and relationships between other attributes such as body size, shape, age, hormonal quality etc. are not clear cut. There are some mixed and sometimes contradictory findings. It is likely that cultural factors interfere when trying to establish such relationships since, although the range of a speaker's voice is biologically constrained by the anatomy of the larynx, cultural norms may dictate whereabouts in this range a speaker chooses to "place" their voice. People learn to use their voice in ways that are culturally determined, for example, Japanese women were traditionally expected to speak more politely than men and expressed this by placing their voice in the upper part of their range (Krauss et al, 2002) and there is thus therefore evidence of greater sex differences in fundamental frequency between Japanese men and women (Loveday, 1981). However, as gender roles have become less differentiated in Japanese society, there is now less evidence of this (Horvat, 2000). There is also some evidence that English speaking men place their voice low in the range of what is possible whereas English speaking women favour the middle of their range (Gradol & Swann, 1983).

Further, the voices presented in the studies reported here were reciting numbers in their normal speaking voice in a laboratory. However, both fundamental and formant frequencies may be deliberately modified. For example, men may retract their larynges (in order to lengthen the vocal tract) to make their voices sound deeper (Laver, 1980). An approximate 10% increase or decrease is possible by raising or lowering the larynx and by protruding or retracting the lips. It would be of particular interest and relevance to the ‘size exaggeration’ theory to examine momentary deepening of the voice in competitive encounters with other males.

7.1.2 Multiple signals across modalities

This thesis attempted to examine the role of the voice in the context of other cues to attraction – specifically facial cues since usually (although not always) listeners are able to both see and hear other individuals with the notable exception of telephone conversations. Further, integration of information from the voice and the face is thought to play a central role in human social interactions (Campanella & Belin, 2007) although most evolutionary researchers have tended to examine such traits in isolation.

Study 5 of this thesis had two primary aims; to examine the putative relationship between visual and vocal attractiveness and visual and vocal dominance in men and also to examine the relative importance of visual and vocal cues to overall attraction and dominance.

Collins & Missing (2003) found that women with more attractive faces also had more attractive voices as judged by men. However, findings are mixed with regard to the relationship between visual and vocal attractiveness in human males. Results of Study 4 and 5 of this thesis found no relationship between the attractiveness of male voices and faces contradicting the findings of Saxon et al. (2006) but in agreement with Collins & Missing (2003) and Zuckerman et al. (1995). Likewise the relationship between vocal and visual dominance remains equivocal with conflicting findings between the results of Study 4 and 5 of this thesis.

If vocal and facial attractiveness and dominance are related in males, features of both may be “back up” signals of the same quality. For example, since the large masculine features of the adult male face and fundamental frequency are both related to testosterone then they may both signal immunocompetence and hormonal quality. If, however, vocal and visual attractiveness are not related it is possible that features of the voice and the face constitute “multiple” messages each signalling something different.

In Studies 5a and b of this thesis the relative importance of vocal and visual cues to attraction were examined for the first time. The results demonstrated that facial cues have a much greater influence on overall attractiveness judgements than do vocal cues, indeed the results of Study 5a, suggested that the visual process may actively dominate or inhibit the auditory process in attractiveness judgements. However, results also suggested that vocal cues influence attributions of dominance to a greater extent than do facial cues.

Puts et al. (2007) suggested that a deep voice appears to signal dominance more effectively than it increases attractiveness judgements. This proposal is based on a comparison of effect sizes in which a manipulation of fundamental and formant frequencies affected judgements of physical dominance nearly fifteen times more than they affected female judgements of attractiveness (Puts et al. 2006). Puts et al. (2007) speculated that men's voices may have evolved primarily as dominance signals and that women secondarily evolved a preference for aspects of men's voices that conveyed information about mate quality. The findings of Study 6a and b of this thesis in which the voice was found to contribute considerably more to attributions of overall dominance when multiple cues were available than the face which was found to contribute little to overall attractiveness judgements would tend to support this proposition.

The studies reported in this thesis suggest that it is important to consider the voice within a framework of multiple cues and that the perceptual processes of different modalities may interact in very complex ways when making judgements about individuals.

7.2 The Immunocompetence Hypothesis revisited

In the Introduction to this thesis, section 1.4.1 c) provided an outline of the Immunocompetence Handicap Hypothesis and some evidence from non-human species in support of it. However, despite this evidence, Roberts et al. (2004) pointed out that the evidence linking increases in androgen levels with immunosuppression, an underlying assumption of the hypothesis, was equivocal. They conducted a meta-analysis of 36 data sets from 22 separate studies involving birds, reptiles and mammals. With all taxa combined, experimental studies involving testosterone supplementation demonstrated that treated males suffered higher parasite loads and reduced immune function, supporting the Hypothesis. However, when they controlled for the non-independence of studies, testosterone did not appear to act as an immunosuppressant, and certainly within mammals the evidence was very weak (although only 5 studies were included). They recommended that robust tests of the hypothesis require further well-designed manipulations of testosterone within natural variation of physiological levels, combined with biologically relevant and multiple tests of immunity in many more species.

An alternative way of addressing the Immunocompetence Hypothesis is to consider the effects of immune activation upon testosterone. In a recent meta-analysis Boonekamp et al., (2008) considered 13 studies (incorporating 600 males from 6 different species) involving *in vivo* immune challenge and subsequent plasma testosterone measurement. They reported that immune challenge did indeed suppress testosterone, and despite considerable heterogeneity among effect sizes, those for birds and mammals were both significant. The authors concluded that the Immunocompetence Hypothsis is supported in that there appears to be a trade-off between immunocompetence and sexual signalling, though this trade-off is generated more by the effect of immune activation on testosterone, rather than the other way around.

Whilst caution should thus be shown (see Getty 1998, 2002), it seems reasonable to conclude that within various animal species, certain male physical characteristics may provide ‘honest’ signals to female appraisers. A key question for this thesis is to what extent such a conclusion holds true for humans.

One area of research that has received considerable attention relates to the extent to which male facial features in humans serve as honest signals. Thornhill and Gangestad (1993) speculated that human male faces would serve as honest advertisements for health, and in particular parasite resistance. Support for their hypothesis was provided by Shackelford and Larsen (1998) who found some evidence that facially attractive individuals were healthier than unattractive individuals. Additional support for links between male facial attractiveness and health has come from Grammer and Thornhill (1994) and Jones et al. (2001) although other researchers have failed to find such clear links (see Kalick et al., 1998; Weeden & Sabini 2005).

Other studies have focussed on facial masculinity/dominance, and in particular on the ‘hormone markers’ (e.g. jaw, chin, brow ridges) that are thought to develop under the actions of testosterone at puberty (Enlow, 1996). Mueller and Mazur (1997) showed that dominant facial appearance within a cohort of military officers was a key predictor of subsequent rank attainment and reproductive success. In terms of reproductive quality, Soler et al. (2003) assessed relationships between male facial attractiveness and semen quality. In their study 66 males provided a semen sample and had their faces rated by females; facial attractiveness ratings were positively associated with semen quality.

Females may be attracted to such faces because these facial characteristics signal masculinity and dominance, factors that may relate to health and/or immunocompetence, but might also relate to success in intrasexual conflict. In support, Penton-Voak & Chen (2004) constructed composite male facial pictures from males who had been measured as being low or high in circulating testosterone. Females rated these composites for masculinity and attractiveness and the high-testosterone pictures were judges to be more masculine, though not more attractive. More recently Fink et al. (2007) showed that the faces of stronger males (as measured by grip strength) were rated as being more dominant, masculine and attractive.

However, Boothroyd et al. (2005) noted that female preferences for masculinity in male faces might reflect attraction to masculinity rather than towards immunocompetence. In their studies, females viewed composite male faces transformed to alter apparent age, health, and masculinity. Links were found between preferences for age and masculinity but not for health and masculinity, suggesting that facial masculinity is not being used by females as a proxy for health. Artificially aging the faces led to increased perceptions of masculinity and vice versa. Increasing masculinity decreased perceptions of health, or had no effect but increasing health increased perceptions of masculinity. The authors concluded that apparent facial health in male faces may influence perceptions of attractiveness independently of facial masculinity and thus an immunocompetence explanation of female attraction to male facial masculinity was not supported.

The evidence for male facial characteristics acting as honest signals remains equivocal and it is likely that females are utilising multiple signals to make their decisions. This thesis, and researchers in the area of vocal research, rely heavily on Collin's (2000) proposition that low fundamental frequency provides an honest signal of genetic quality in line with the Immunocompetence Hypotheis suggesting that only individuals with superior immunocompetence (i.e. those with immune systems able to bear the ravages of elevated testosterone) will be able to display low fundamental frequency. In support, it should be noted that there is some evidence that testosterone is deleterious to the immune system in human males. Angele and Faist, (2000) reviewed clinical and experimental studies showing that male sex steroids depress the immune system following trauma, while female sex steroids enhance the immune response, therefore low testosterone and high estradiol is immunoprotective. In line with these findings, I have unpublished data suggesting that females rate male voices with low fundamental frequency as significantly more healthy than those with high frequency. However, in the study by Apicella et al. (2007) examining vocal pitch in an evolutionary relevant population (previously reported see section 7.0), although fundamental frequency predicted reproductive success and the number of offspring fathered it did not predict offspring mortality. It would be of future interest to examine the relationship between fundamental frequency and apparent health more closely and between fundamental frequency and actual health more directly.

To review, a preference for fundamental frequency may be due to advertised immunocompetence as proposed by Collins (2000) and further studies examining the relationship between fundamental frequency and both apparent and actual health may help to support this. Further research examining the relationship between testosterone and immunity may also shed light on the assumptions of the Immunocompetence Hypothesis. However, as Boothroyd et al. (2005) point out in the facial attraction literature, alternative explanations such as dominance and high status should also be considered particularly given the consistent relationship between fundamental frequency and ratings of dominance.

7.3 Ecologically valid stimuli

A potential limitation of this thesis is that natural voices were employed as stimuli rather than experimentally manipulated voices in an attempt to use ecologically valid stimuli. This approach has become more common in the animal literature where there has been a shift in recent years from artificial stimuli to biologically natural and meaningful stimuli in playback studies. There are obviously advantages and disadvantages involved with both methods, however, common findings using both methods can only add strength to general conclusions drawn. With regard to the vocal stimuli that were employed themselves, some researchers have used vowel sounds

(Collins, 2000; Feinberg et al., 2004, 2006), unscripted passages (Puts et al., 2005; 2007) and others have used samples of speakers reciting the numbers 1-10 (Ellis, 1967; Hughes et al. 2004). In this thesis vowel sounds were used in Study 1 examining the relationship between acoustic measures and physical characteristics, however, it became apparent that participants used as judges in ratings studies found it very difficult to listen to this type of stimuli – the recorded voices were reported as sounding unnatural and obscure. Thus, in further studies the stimuli presented consisted of male voices uttering the numbers 1-10 in order to produce stimuli that were neutral and of comparable content and thought to be as ecologically valid as possible but at the same time attempting to control for aspects of speech contained in longer passages of continuous speech that may contain confounding variables. In addition, the face stimuli used in Studies 5 and 6 were static photographs and, as has already been mentioned, dynamic images with speech synchronised to movement would provide more ecologically valid stimuli in future studies. Further, there are properties of the voice such as jitter and shimmer (which perceptually correspond to voice roughness) that have not been examined here since there is considerable disagreement in the literature about standard measurement of such variables (eg. Pinto & Titze, 1990), although they may have an influence on perception of voices since, for example, shimmer is related to vocal fold health and may therefore influence attractiveness ratings.

7.4 **The use of parametric statistical tests on data from Likert-type rating scales.**

The use of parametric statistical tests on data from Likert-type rating scales employed in this thesis requires some justification. Parametric statistical tests make assumptions about the interval level properties of the data and whilst they are commonly used in current literature to analyse data from studies using rating scales, there is some argument among researchers about their appropriateness. However, Gregoire & Driver (1987) concluded that there was little reason to prefer non-parametric over parametric tests following a Monte-Carlo study on data from a Likert-type rating scale where equal differences on the scale did not represent equal differences on the underlying variable.

7.5 Conclusions

At the start of this research programme only one paper had been published examining the role of the male voice in human courtship. Since that time the examination of the deep voice of the human male as a sexually selected trait has attracted a great deal of attention. The null hypothesis being, of course, that the deep voice of the human male is not a sexually selected trait. My own work and that of other researchers in the area of evolutionary psychology suggests that the deep voice of the human male may indeed be a sexually selected trait that has been modified over the course of human evolution meeting the five criteria for demonstrating sexual selection in communication proposed by Snowdon (2004). The voice of the human male is a sexually dimorphic trait that also displays within-sex variability that can be easily perceived by others. Evidence suggests that females display a preference for males with deep voices when considering potential short-term partners and there is growing evidence that deep voices also intimidate other males by indicating the dominance of the speaker. Finally, recent evidence also suggests that males with deep voices enjoy greater reproductive success.

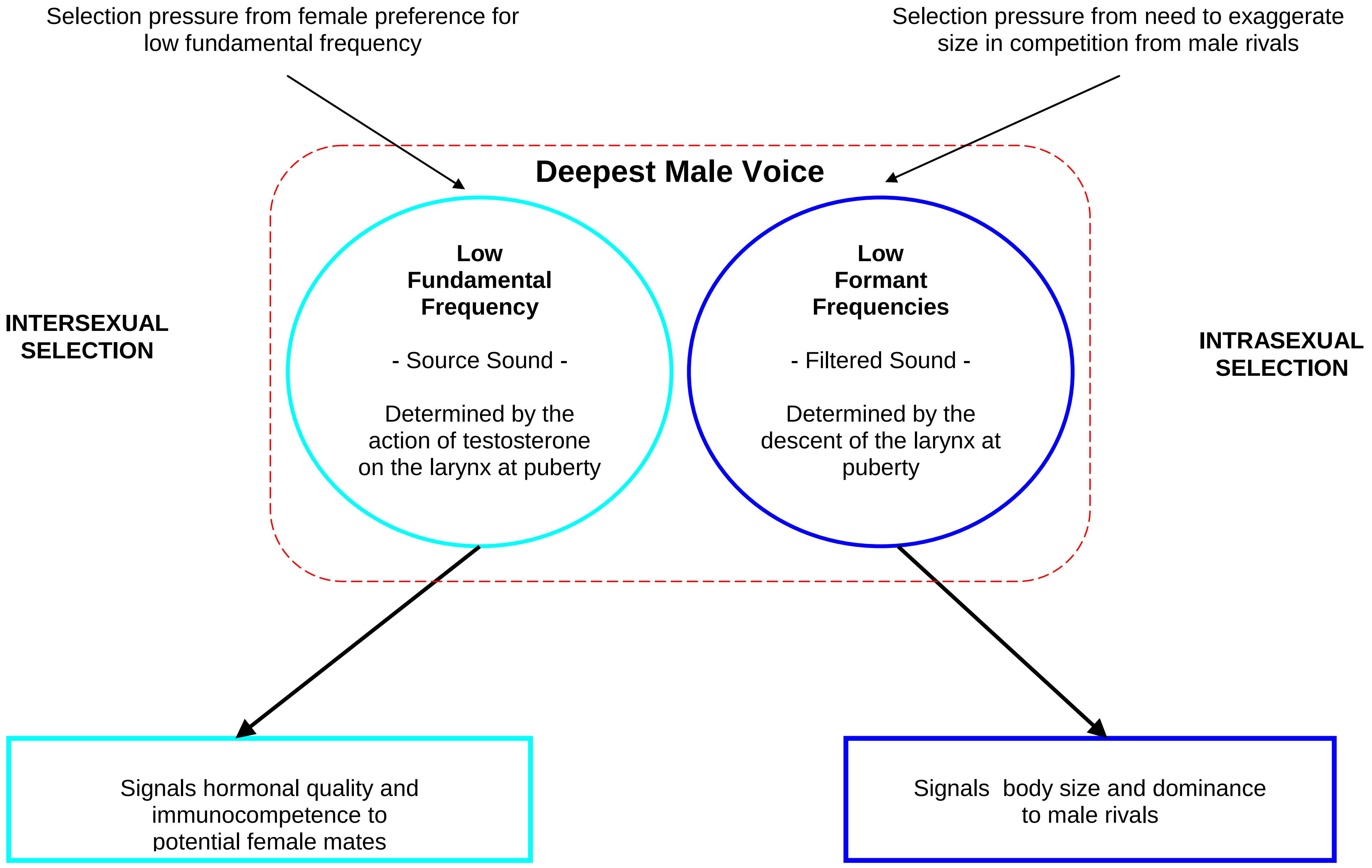
Most previous research has focused on the deep voice of the human male without considering the importance of examining the relative contribution of both fundamental and formant frequencies which I believe may be central to the understanding of the function of a deep voice. Further research is necessary to tease apart the two components of a deep voice - formant frequencies and fundamental frequency - which I speculate may have evolved distinctly. The recent development of STRAIGHT software that is reliably able to manipulate formant and fundamental frequencies independently of one another will no doubt prove useful in future research.

The descent of the larynx which lowers formant frequencies in human males may have evolved through directional selection in order for males to exaggerate size in relation to intrasexual selection (Fitch & Reby, 2001); whereas the sexual dimorphism of fundamental frequencies may have evolved under disruptive selection pressure in order for both males and females to attract the opposite sex by advertising their hormonal quality in relation to intersexual selection (see figure 7.b).

Although the question of whether vocal and visual attractiveness and dominance are related remains equivocal, by examining the voice within a framework of multiple signals, the results of this thesis suggests that the male voice is more important to judgements of dominance than facial cues and that the face is more important to attributions of attractiveness than the face. This research programme has thus highlighted the limitations of examining such cues in isolation.

Finally, research examining the evolution of the male voice as a sexually selected trait is in its infancy compared to research examining other such traits such as features of the face. Much more remains to be known about the evolution of a deep voice in the human male and it remains a fertile field for further research.

Figure 7b - The evolution of a deep male voice



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Appendix i

Evans, S., Neave, N., Wakelin, D. & Hamilton, C. (2006). Relationships between vocal characteristics and body shape in human males: an evolutionary explanation for a deep male voice. Biological Psychology. 72, 160-163.

ABSTRACT

A deep male voice may play a role in courtship and competitive behaviours in humans by attracting female mates and indicating body size to male competitors. The current correlational study investigated the relationship between vocal measures (fundamental and formant frequencies) and both body size and shape using a non experimental design with correlational analysis. Vocal samples and physical measures were obtained from 50 heterosexual male volunteers. A significant negative relationship was found between fundamental frequency and measures of body shape and weight. Further, a significant negative relationship was found between formant dispersion (the relationship between successive formant frequencies) and measures of body size as well as body shape. Findings are discussed in relation to the 'good genes' model of sexual selection and the size exaggeration theory of laryngeal descent.

Keywords: Fundamental frequency, formant frequencies, size exaggeration, attraction.

1. INTRODUCTION

There are two acoustic components to the voice, fundamental frequency (pitch) and formant or resonant frequencies. According to the Source-Filter Theory of Speech Production (Muller, 1848; Fant, 1960), fundamental frequency is determined by the vibration of the vocal folds (source), and formants, which modify this source sound, are determined by the size and shape of the vocal tract (filter) and by moving the articulators including the tongue, lips and soft palate etc. (Jenkins, 1998; Fitch, 2000).

An adult male voice is considerably deeper than that of an adult female or prepubescent child due to changes that take place in the larynx during puberty. Levels of circulating testosterone lengthen and permanently thicken the vocal folds, lowering fundamental frequency (Jenkins, 1998). A simultaneous but independent secondary descent of the larynx results in a lowering of formants and less formant dispersion (the formants are closer together) (Fitch and Giedd, 1999). The acoustic effect of both of these changes together, contributes to a more imposing, deep voice in an adult male. It is important to remember that fundamental frequency and formant frequencies are independent of one another. Whilst the concept of pitch is easily understood, formants are more difficult to conceptualise, they are another component of "timbre" or voice quality and are highly audible and salient (Fitch, 2000).

Research has shown that the deepening of the male voice is a secondary sexual characteristic that may play a role in attracting female mates. Collins (2000) reported that women prefer the voices of men with low fundamental frequencies, and suggested that since fundamental frequency is determined by testosterone, a deep male voice may be providing potential female mates with an honest signal of immunocompetence and hormonal quality, in line with the 'good genes' model of sexual selection.

A deep male voice may also be an indicator of body size and body shape. In the context of this paper and specifically the evolutionary theory discussed, it is important to distinguish between these two physical constructs. Body size refers to height and weight which may be implicated in indicating size to male competitors, whereas body shape refers to body configuration including measures of body circumferences and ratios derived from these measures (e.g shoulder-hip ratio, waist-to-hip ratio). Body shape may be implicated in providing a signal of immunocompetence and hormonal quality to female mates since it is dependent on testosterone. As early as 1872 Darwin proposed a link between body size and fundamental frequency, although subsequent studies have failed to find a relationship (Kunzel, 1989; Lass and Brown, 1978; Sawashima et al., 1983). Indeed, a study examining the ability of listeners to judge speaker height and weight from speech samples found that low fundamental frequency was incorrectly taken to indicate body dimensions (van Dommelen and Moxness, 1995). Similarly, in Collins' (2000) study in which men with deeper voices were judged as more attractive by female judges, judgements were also made about their physical characteristics such as that men with deep voices were assumed to be heavier, older, more likely to have a hairy chest and a muscular body type. However, the judges were wrong. More recently Hughes et al. (2004) reported a relationship between opposite sex ratings of vocal attractiveness and shoulder-hip ratio in males. It is possible that fundamental frequency indicates body configuration or body shape rather than body size but this prediction needs to be tested with a direct measure of fundamental frequency.

Fitch and colleagues have proposed that formant dispersion rather than fundamental frequency forms an acoustic cue to body size. Formant dispersion is the relationship between successive formant frequencies, for example, small formant dispersion means that the formant frequencies are closer together. There is evidence of a correlation between body size, vocal tract length, and formant frequencies in non-human primates (Fitch and Giedd, 1999), the formant frequencies of larger individuals being closer together (Fitch, 1997). Fitch and Giedd (1999) also found a strong positive correlation between body size and vocal tract length in a magnetic resonance imaging study of 129 male and female humans. In a study by Feinberg et al. (2005) in which vocal frequencies of natural voices were manipulated using computer software, voices with original fundamental frequency but increased apparent vocal tract length (smaller formant dispersion) were rated by female judges as being larger, more masculine, and older, than voices with combined lower fundamental frequency and increased apparent vocal tract length. These findings suggest that formant dispersion is the specific cue to body size but perhaps listeners, unable to explicitly distinguish between fundamental and formant frequencies, incorrectly attribute fundamental frequency as a cue to body size. Indeed, the layperson is probably familiar with the terms 'pitch' and perhaps ‘fundamental frequency,’ but most have no knowledge of ‘formant frequencies’ at all.

For many years it was believed that a descended larynx (which lowers formant frequencies because of an increase in the length of the vocal tract) was uniquely human and that this descent was a necessary prerequisite for the development of speech and language. However, Fitch and Reby (2001) found that the descended larynx is not unique to humans and proposed that the original selective advantage may have been to enable individuals to duplicate the vocalisations of larger ones and thus exaggerate their size. This explanation proposes that the original selective advantage of a lowered larynx was to exaggerate size and had nothing to do with speech. Fitch and Giedd (1999) further proposed that the secondary descent of the larynx in human males represented a sexually dimorphic adaptation to give adult males a more imposing voice relative to females and prepubescent males. Fitch’s size exaggeration theory suggests that formant frequencies may play an important role in male-male competition for mates.

Collins (2000) found no relationship between any characteristics of the voice and physical measures of the body in a sample of Dutch male speakers. However, a study by Gonzalez (2004) found a weak relationship between formant frequencies and the height and weight of young (20-30 years) Spanish male speakers. The purpose of the current study was to investigate the relationship between various measures of both body size and shape and both fundamental frequency and formant dispersion in a sample of English speaking males from a wider age range. Collins (2000) identified that most studies involving judgement of voices involved recordings of spoken words or sentences that might allow confounding variables such as accent or speech patterns to influence results. In order to minimise these effects, we used methodology employed by Collins and recorded male voices reciting vowel sounds only. Vowel sounds also provide a particularly clear measure of fundamental and formant frequencies. We predicted that fundamental frequency in males would be related to body shape and that formant dispersion would be related to body size.

2. MATERIAL AND METHODS

2.1 Participants

Participants were recruited on a voluntary basis from an opportunity sample at the Northumbria University campus and the general population. 50 self-reported heterosexual males aged between 18-68 (mean = 29.08, sd = 12.31) took part in the study. All participants reported that they had not suffered any damage, or had surgery to their nose or throat or broken any bones associated with the physical measures taken. English was the first language of all participants.

2.2 Materials

2.2.1 Measures of vocal characteristics and analysis

All voices were recorded using a PC with a Logic headset microphone onto Steinberg WaveLab 5.0 software. The headset microphone ensured that all speakers were at a constant distance from the microphone (10 cms) when recording was taking place and a constant sound recording level was used.

Each participant was asked to repeat the English vowels “a”, “e”, “i” and “o”. Praat software v.3.9.2 (Boersma & Weenink, www.praat.org) was used for vocal analysis. The mean fundamental frequency of the vocal sample was calculated using the autocorrelation method (analysis parameters were modified for adult male - minimum pitch 75 Hz/Maximum pitch 300 Hz). Mean values for Formants 1-4 were calculated for both vocal samples using the Burg Linear Predictive Coding Algorithm (default parameters were used except maximum formant was modified to 5000 Hz suitable for adult males). Formant dispersion was calculated as (F3-F2)+(F2-F1)/2 (as in Feinberg 2005) because the fourth frequency was not present in all individuals.

2.2.2 Physical measures

Physical measures were taken using an anthropometric body measurement tape. Skull circumference (circ.) was measured above the eyebrow; neck circumference was measured around the neck at the laryngeal prominence (Adam’s apple); shoulder circumference was measured at the widest point of the shoulders between the acromion bones with the individual’s arms at their side. Chest circumference was measured at the widest point; waist circumference was measured at the level of the umbilicus and hip circumference was measured at the greatest girth around the hips and buttocks. Height was measured using a stadiometer and weight using digital scales. shoulder-hip ratio, shoulder-waist ratio, waist-hip ratio and body mass index were derived from these measurements. A measure of maximal peak expiratory flow was taken using a spirometer as a measure of lung capacity.

2.3 Procedure

All participants gave their informed written consent and the procedure was passed by the School of Psychology & Sport Sciences Ethics Committee. Participants were tested individually and firstly asked to complete a brief, biographical questionnaire. All physical measurements were then taken as well as measures of height, weight and lung capacity. Participants voices were then recorded before they were debriefed.

3. RESULTS

Descriptive Statistics. Results of the vocal analysis found that the mean fundamental frequency of the vocal samples was 106.54 Hertz (Hz) (SD =16.21) with a range of between 75.54 Hz and 159.55 Hz. The mean formant dispersion was 1651.71 Hz (SD = 88.09) with a range of between 1497.79 Hz and 1720.78 Hz. Table I provides a summary of the mean, standard deviation and range of the physical measures taken. The physical measures were comparable to those found in other studies where comparisons could be made (Hughes et al., 2004; Gonzalez, 2004).

Measure	**Mean**	**SD**	**Range**
Body Size:			
Weight (kg)	81	12.94	62.70-111.20
Height (cm)	179.82	6.22	165-195

Body Mass Index	27.27	7.48	18.93-54.27
Peak Expiratory Flow (l/min)	466.50	144.15	84-775
Body Shape:			
Skull circ. (cm)	57.99	1.59	55-62
Neck circ. (cm)	38.92	2.32	34-46.5
Shoulder circ. (cm)	108.78	7.60	96-129.5
Chest circ. (cm)	96.79	8.74	82-117
Waist circ.(cm)	89.74	11.18	74-114
Hip circ. (cm)	99.29	7.48	84-115
Shoulder-Hip Ratio	1.10	.08	1.07-1.14
Shoulder-Waist Ratio	1.12	.12	1-1.17
Waist-Hip Ratio	1.12	.12	1.01-1.14

Table I - Mean, standard deviation and range for the physical measures taken

Correlations. A Pearson Product-Moment Correlation was carried out using SPSS software (v.12.0.1) for mean fundamental frequency, formant dispersion and age. A significant positive relationship was found between fundamental frequency and age of participant ($r = .43$, $p = .002$). Younger individuals had lower fundamental frequency. Since age was identified as a possible confounding factor, all further analyses of fundamental frequency were carried out using partial correlations (r_p), holding age constant. No significant relationship was found between age and formant dispersion.

With regard to body size, no significant relationship was found between the mean fundamental frequency of the vowels and height, lung capacity or body mass index although weight was significantly negatively correlated to mean fundamental frequency ($r_p = -.34$, $p=.02$), heavier individuals had lower fundamental frequency Weight and height were significantly negatively correlated with formant dispersion, ($r = -.43$, $p = .002$; $r = -.32$, $p = .024$ respectively) demonstrating that heavier and taller individuals had smaller formant dispersion. No significant relationship was found between formant dispersion and body mass index or lung capacity.

With regard to body shape, no significant relationship was found between mean fundamental frequency and skull, neck, waist, and hip circumferences. However, shoulder circumference was significantly negatively correlated with mean fundamental frequency, ($r_p = -.29$, $p = .04$) and chest circumference was significantly negatively correlated with mean fundamental frequency, ($r_p = -.28$, $p = .04$). Shoulder-hip ratio was also significantly negatively correlated with mean fundamental frequency, ($r_p = -.49$, $p < .001$) Larger shoulder and chest circumference as well as shoulder-hip ratio indicated lower fundamental frequency. No significant relationship was found between waist-hip ratio, shoulder-waist ratio and mean fundamental frequency.

No significant relationship was found between skull and hip circumferences and formant dispersion. However the following circumferences were significantly negatively correlated with formant dispersion: neck, ($r = -.50$, $p < .001$); shoulder, ($r = .-56$, $p < .001$); chest, ($r = -.45$, $p = .001$) and waist, ($r = -.39$, $p = .005$). Larger circumference indicated smaller formant dispersion. Shoulder-hip ratio was also significantly negatively correlated with formant dispersion ($r = -.39$, $p = .006$) although there was no significant relationship between fundamental frequency and shoulder-waist ratio and waist-hip ratio.

4. DISCUSSION

In line with our prediction, this study found a significant negative relationship between the fundamental frequency (pitch) of the male voice and measures of body shape including shoulder and chest circumferences and shoulder-hip ratio. Low fundamental frequencies indicated individuals with larger body shape, specifically upper body musculature. Fundamental frequency was also related to one measure of body size, weight was significantly negatively correlated with fundamental frequency. Further, a significant negative relationship was also found between formant dispersion and body size (weight and height). Interestingly, a relationship was also found between formant dispersion and body shape (neck, shoulder, chest and waist circumferences and shoulder-hip ratio). Small formant dispersion indicated males with larger body size and shape.

First, with regard to body shape and fundamental frequency, findings of a relationship between low fundamental frequency and large body shape, in particular a large upper musculature, suggests that a speaker’s fundamental frequency provides a cue to body configuration. Low fundamental frequency and sexually dimorphic body configuration are both determined at puberty by the action of testosterone and may therefore be honest multi-channel signals of genetic quality and hormonal health to potential female mates.

Second, with regard to formant frequency and body size, Gonzalez (2004) found a weak relationship between formant frequencies and height and weight and Sachs et al. (1972) found a negative correlation between vowel formant frequencies and height. The current study supports these findings although the correlation between formant frequencies was stronger for weight than height. However, the relationship between weight and formant dispersion must be viewed with caution, since the prevalence of overweight individuals in Western society may weaken any correlation (Fitch, 1999).

Both Gonzalez (2004), and the current study, found a weaker relationship between body size and formant frequencies in humans than Fitch (1997) found in rhesus macaques. One possible explanation of a weaker relationship between formant frequency and body size in humans than other primates is that the secondary descent of the larynx in human males disassociates vocal tract length from skeletal and body size (Fitch, 1997). Gonzalez (2004) found a stronger relationship between formant frequencies and body size in women than males, supporting this proposal.

Thirdly, the current study also found a correlation between formant dispersion and body shape not previously reported. Body shape or shoulder-hip ratio and fundamental frequency are thought to be largely dependant on levels of testosterone present at puberty. The control mechanism by which the larynx is lowered in human males is currently unknown, however these results imply that testosterone may also play a role here although it is most likely that these changes in the larynx are under the influence of an interaction between both sex and growth hormones as suggested by Fitch (1997).

Finally, once the age of participant was controlled for, the current study involving English speaking males found a correlation between fundamental frequency and weight not previously reported. One possible explanation for this finding is that, although the range of a speaker's voice is constrained by the anatomy of the larynx, cultural norms may dictate whereabouts in this range a speaker chooses to "place" their voice. People learn to use their voice in ways that are culturally determined, and there is some evidence that English speaking men place their voice low in the range of what is possible (Gradol and Swann, 1983).

It is suggested that male vocal characteristics play a role in attracting female mates and also in competition with male rivals. Many previous studies have found his to be true in animals (for review see Kelley and Brenowitz, 2002). Fundamental frequency and formant dispersion are independent components of a deep voice in a human male (Fitch, 2000) which we propose may be providing different cues to different listeners. On the one hand, fundamental frequency may attract female mates by providing an honest cue of hormonal quality and, on the other hand, formant dispersion may signal body size/shape to intimidate male rivals in competition for female mates.

In conclusion, results of this study suggest that a deep voice indicates aspects of body size and shape in the human male and may have evolved because it plays a role in human mating and competitive behaviours by signalling hormonal profile to female mates and indicating overall body size to male rivals Further research will be necessary to examine male and female perceptions of voices and the relative importance of both visual and vocal cues in the context of courtship and competition and we are currently addressing these research questions.

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Appendix ii

Evans, S., Neave, N., Wakelin, D. & Hamilton, C. (2008).The relationship between testosterone and vocal frequencies in human males. Physiology & Behavior. 93, 783-788.

Abstract

We investigated relationships between circulating levels of salivary testosterone and the fundamental and formant frequencies of male voices in a sample of forty healthy adult males, who recorded their voices and provided saliva samples at 9am, 12 noon and 3pm on a single day. The relationship between 2D:4D ratio as a putative biomarker of prenatal testosterone and vocal parameters was also explored. Results supported previous findings for a negative relationship between circulating levels of testosterone and fundamental frequency, with higher testosterone indicating lower fundamental frequency, although the magnitude of the relationship was larger than previously observed. Some limited evidence for a relationship between circulating testosterone and formant dispersion was also found, although this did not reach significance. Diurnal variation in testosterone and fundamental frequency, but not formant dispersion was reported, together with a trend towards an association between the fall in testosterone and the rise in fundamental frequency. Finally, there was no relationship between 2D:4D and the vocal parameters. It is thought that male voices may have deepened over the course of evolution in order to signal dominance and/or to increase the speaker's attractiveness. Findings confirm that vocal frequencies may provide an honest signal of the speaker's hormonal quality.

Keywords: Testosterone; diurnal variation; voice; fundamental frequency; formant dispersion; male

1. Introduction

Evidence suggests that primates and many other animals make mating decisions based on androgen-mediated acoustic cues and that such cues are an important factor in competitive behaviours (see [1] and [2] for reviews), however, it is not until recently that attention has turned to the influence of the human voice, or more specifically certain acoustic frequencies of the voice, upon human attraction and dominance behaviours. It is thought that male vocal frequencies may provide 'honest' signals to potential female mates and male rivals of both hormonal quality [3], and aspects of physical quality (eg. body shape and size [4]).

According to the Source-Filter Theory of Speech Production [5,6] the human voice consists of two independent acoustic components, fundamental frequency (F_0), and formant (or resonant) frequencies. The former is determined by the vibration of the vocal folds, and forms the primary determinant of the perceived pitch of a vocalization. The latter are determined by the size and shape of the vocal tract, and by the movement of the articulators. Prior to puberty there are small differences between male and female voices, with boys reported to have lower formants [7] but such differences become greatly magnified during puberty and adulthood.

At puberty, changes in the male larynx permanently lower fundamental frequency [8]. The average fundamental frequency in an adult male is approximately 100 Hertz (Hz), while it is around 213 Hz in an adult female [7]. A secondary descent of the larynx also produces lower formant frequencies and less formant dispersion (D_f); the formants are closer together [9]. The acoustic effect of these, simultaneous but independent, physical changes contributes to a deeper, more imposing voice in an adult male relative to a prepubescent child or adult female.

Experimental animal studies have shown that androgen stimulation has direct effects upon the larynx, influencing acoustic changes, e.g. [10]. The same structure appears to undergo similar changes during puberty in humans, for example, Kahane [11] described preadolescent and adolescent laryngeal growth changes in human cadavers aged 9-19, and noted that the most striking developmental change was the enlargement of the thyroid cartilage over the course of puberty. The vocal folds also demonstrated significant growth in males, increasing by 63% from pre-puberty to puberty; female vocal fold growth was 34% over the same period. In living volunteers, Fitch and Giedd [9] assessed the development of the vocal tract using magnetic resonance imaging. They reported a significant difference between male and female vocal tract morphology, notably in the length of the vocal tract and in the relative proportions of the oral and pharyngeal cavities, which were not evident in children.

With regard to the association between hormonal changes and vocal tract development, Harries and colleagues [12] recorded both singing and speaking frequencies, and salivary testosterone over a one-year period in a group of 13-14 year old boys passing through the established Tanner stages of puberty. Abrupt vocal changes were observed between Tanner stages III and IV and while circulating testosterone levels were not related to these changes, testicular volume was, i.e. larger testis volume was associated with lower voice pitch.

As vocal changes appear to be completed after puberty there is no apparent reason to suppose that vocal frequencies will show any relationship to circulating androgen levels later in life. However, a small number of studies have investigated whether testosterone, as measured by circulating levels of free testosterone (T) in salivary samples, continues to be related to vocal parameters such as fundamental frequency and formant dispersion in adult males. In the first study to explore the relationship between sex steroids and the male voice, Meuser & Neischlag [13] reported lower testosterone/estradiol ratios among tenors than in baritone and base singers. Two further studies [14] and [15] found a negative correlation between circulating testosterone and fundamental frequency in samples of young men, such that higher levels of testosterone were associated with lower fundamental frequency. More recently, a study by Bruckert and colleagues [16] reported no relationship between testosterone and fundamental frequency, but did find that male speakers with small formant dispersion (formant frequencies that are closer together) had higher levels of circulating testosterone. However, these researchers used a cotton-based material to collect the samples, and problems with this methodology have been reported [17].

Diurnal variation in salivary and serum testosterone concentrations in adult men with a peak in the morning and a nadir in the early evening have been reported in many studies eg. [18], although previous studies examining the relationship between vocal parameters and circulating testosterone have not controlled for time of day. One of the primary aims of the current study therefore was to replicate the examination of this relationship, but to employ multiple sampling times of both vocal and circulating testosterone measures across a single day.

In addition, the examination of the relationship between early exposure to testosterone and vocal parameters is incomplete and remains equivocal. The ratio between the second and fourth fingers (2D:4D) has been proposed as a putative marker of prenatal testosterone exposure [19]. While it might be assumed that early androgen exposure might have little influence upon adult characteristics determined by circulating androgen levels during puberty, some studies have revealed that early androgen exposure (as assessed by 2D:4D) might be associated with certain physical characteristics determined during puberty, suggesting that these two surges might be related [e.g. 20,21]. This measure has been used to assess possible relationships between early prenatal testosterone exposure and vocal parameters in adulthood, but with little success. One study [22] found no relationship between a measure of fundamental frequency from continuous speech and 2D:4D ratio. Another study [23] revealed no relationship between subjective measures of vocal attractiveness and 2D:4D ratio. While the evidence thus far appears lacking for a relationship between prenatal androgen exposure and adult voice pitch, this study reassessed such a relationship to provide further clarification.

To summarise, since previous findings for a relationship between early exposure to testosterone (as assessed by the putative proxy 2D:4D) and circulating levels of testosterone and vocal parameters are mixed and therefore equivocal, the current study aimed to replicate the examination of such relationships with the aim of clarification, using more rigorous methodology for the measurement of testosterone and for the first time accounting for diurnal variation.

2. Materials and methods

2.1 Sample

This comprised 40 healthy males aged 18-25 (mean = 20.6 years, SD = 1.81) recruited from student population of Northumbria University. All were self-reported heterosexual, non-smokers with English as their first language. They reported that they were currently not suffering from any chronic diseases or hormonal abnormalities. None were currently suffering from any conditions that might affect their voice (e.g. colds, sore throats etc) and none reported present or previous anabolic steroid use. The sample did not include any shift-workers. They were paid £10 for their participation.

2.2 Procedure

The study received ethical approval by the School of Psychology & Sport Sciences Ethics Committee. During an initial laboratory-based training session, participants gave their written informed consent, completed a brief biographical questionnaire, and their left and right hands were scanned. They then practiced the protocol for providing saliva samples and vocal recordings, and were given the equipment and instructions necessary for them to provide both. As testosterone has been shown to have considerable diurnal variation [18] 3 samples across a single day were collected at 9am, 12 noon and 3pm. Participants returned the voice recorders and saliva samples to the laboratory following the final collection, and were fully debriefed.

2.3 Finger ratio measurement

Right and left hands were scanned using a Canon (LiDE 25) colour flatbed scanner. Participants were instructed to place the palm of their hand in a relaxed position with fingers evenly spaced on the glass of the scanner without applying pressure. The second and fourth fingers were then measured by two independent experimenters from the scanned images. Finger lengths were measured from the basal crease to the proximal tip on the ventral surface of both left and right hand printed images using digital callipers (Mitutoyo Products, UK) accurate to 0.01mm. The mean value of the two experimenter measures was taken for each digit, and 2D:4D ratio calculated accordingly.

2.4 Vocal recordings and analysis

Participants were instructed to provide vocal recordings (counting slowly from 1-10) onto Olympus VN-240PC digital voice recorders at 9am (within 2 hours of waking from an overnight sleep), 12 noon and 3pm on a single day. A tolerance of +/- 10 minutes was permitted. Compliance with the procedure could be confirmed as the voice recorders recorded the time of recording, and all participants demonstrated full compliance (within -3 and +7 minutes). The files were then transferred to a PC and saved as wav files. Praat software v.3.9.2 (Boersma & Weenink, www.praat.org) was used for vocal analysis. The mean fundamental frequency across the vocal sample was calculated using the autocorrelation method (analysis parameters were modified for adult male - minimum pitch 75 Hz/Maximum pitch 300 Hz). Mean values for formants 1-4 were calculated using the Burg Linear Predictive Coding Algorithm (default parameters were used except maximum formant was modified to 5000 Hz suitable for adult males). Formant dispersion was calculated as (F3-F2)+(F2-F1)/2, as described in [24].

2.5 Salivary testosterone collection and analysis

Participants were instructed to provide 3 samples of 5ml of saliva on a single day at 9am, 12 noon and 3pm using Salicaps (ImmunoBiological Laboratories, Hamburg) provided. They were asked to refrain from eating, drinking or brushing their teeth for 30 minutes prior to providing each sample, and to rinse their mouth with water 15 minutes before sample production. Participants were also asked to refrain from strenuous exercise on the testing day. All samples were frozen at -20°C until analysis in line with recommended protocol. Salivary testosterone levels were determined using standard luminescence immunoassay kits (IBL, Hamburg) commonly used for research purposes and the in-vitro-diagnostic quantitative determination of testosterone in human saliva. Each sample at each time point was analysed in duplicate, and a mean of the two measures was used for statistical analysis.

3. Results

Seven individual saliva samples were excluded from statistical analysis as they were not suitable for analysis, for example, results lay outside the range of expected values for the age group concerned or upon visual inspection blood contamination was suspected by the laboratory technician. Likewise ten individual vocal measures were excluded from statistical analyses because of technical difficulties. This explains the variation in sample size across analyses. All statistical analyses were conducted on SPSS 12.0.1 unless otherwise indicated and were two-tailed. Corrections for multiple correlations were not applied because any correlations were predicted to be small based on previous findings.

3.1 The relationship between vocal parameters and circulating testosterone

The three saliva samples taken at 9am, 12 noon, and 3pm, and a daily mean value (the mean of the three samples) were correlated with measures of fundamental frequency and formant dispersion using Pearson's Product Moment correlations. The daily mean value for testosterone was significantly correlated with daily mean values for fundamental frequency ($r = -.512$, $p < .005$), higher testosterone being associated with lower fundamental frequency (see Figure 1). More detailed analysis revealed a significant negative relationship between testosterone and fundamental frequency at 9am ($r = -.506$, $p < .005$) and at 3pm ($r = -.360$, $p < .05$) and a trend towards a relationship between testosterone and fundamental frequency at 12 noon ($r = -.325$, $p > .05$). There was a trend towards significance for a negative relationship between the daily mean for testosterone and daily mean values for formant dispersion ($r = -.310$, $p < .05$), with higher testosterone indicating smaller formant dispersion. More detailed analysis revealed no significant relationship between testosterone and formant dispersion at individual time points.

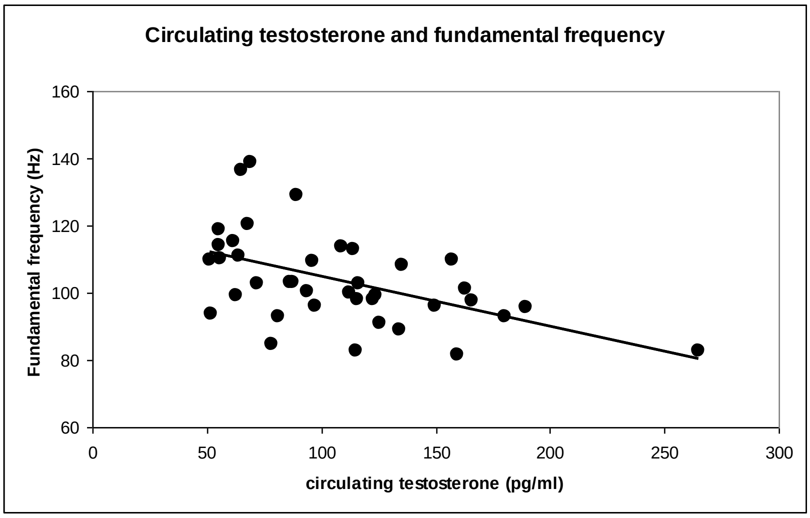

Figure 1 – Relationship between daily means for fundamental frequency and daily means for circulating testosterone ($y=-0.15x+119.58$, $R^2 = 0.26$).

3.2 The effect of time of day on testosterone and vocal measures

One-way within-subject ANOVA's with three levels (9am, 12 noon and 3pm) were carried out to examine the possible effect of time of day on measures of testosterone, fundamental frequency, and formant dispersion. Post-hoc planned comparisons (Bonferroni-corrected for multiple comparisons, $\alpha = .05$) examined differences in measures at 9am, 12 noon and 3pm. There was a significant main effect of time of day on circulating levels of testosterone ($F_{2,68} = 3.79$, $p < .05$), and a significant linear trend ($F_{1,34} = 4.51$, $p < .05$) although there were no significant differences between circulating levels of testosterone at 9am, 12 noon and 3pm. Figure 2a provides the mean values and standard deviations at each time point.

There was also a significant effect of time of day ($F_{2, 68} = 9.92$, $p < .001$) on fundamental frequency, and a significant linear trend ($F_{1,34} = 16.73$, $p < .001$). There was a significant difference between fundamental frequency at 9am and 3pm ($p < .005$) and a trend towards significance for a difference between measures of fundamental frequency at 12 noon and 3pm ($p > .05$). Figure 2b provides the mean values and standard deviations at each time point.

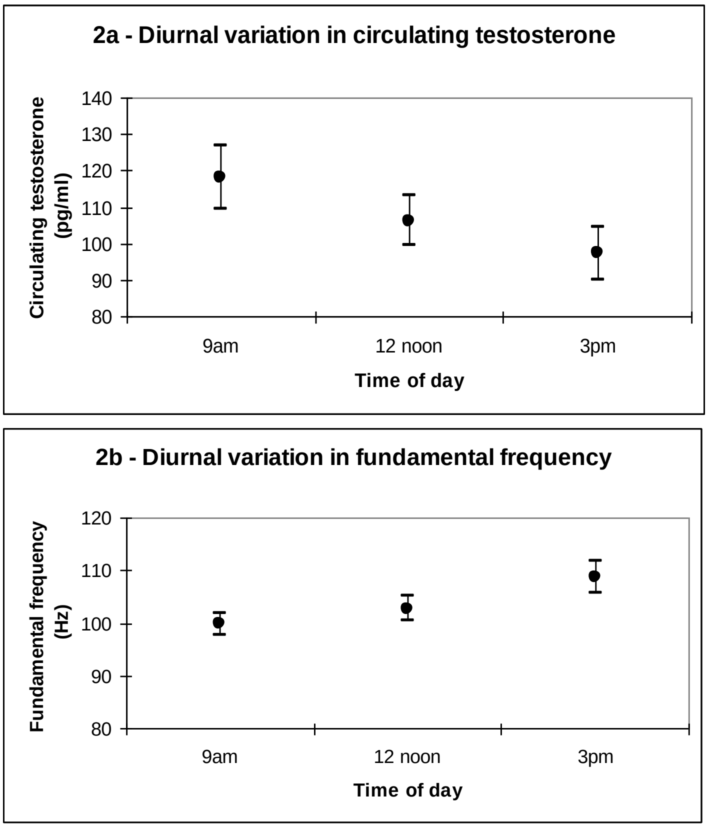

Figure 2 - Diurnal variation in (a) circulating testosterone and (b) fundamental frequency with means +/- SEM.

3.3 The relationship between measures of the slope for testosterone and vocal frequencies.

Using Excel (Microsoft Office XP) the slope statistics were calculated for measures of testosterone, fundamental frequency and formant dispersion as a function of time of day. Spearman rho correlations were then carried out and a trend towards significance for a negative relationship between measures of the testosterone slope and the fundamental frequency slope was observed (rho = -.331, N = 34, $p > .05$ (two-tailed). No other relationships approached significance.

3.4 The relationship between vocal measures and 2D:4D ratio

The concordance between the digit measurements of the two independent experimenters was calculated using Cronbach's reliability analysis which revealed high agreement in measures of the right hand (α = .996) and left hand (α = .993). The technical error of measurement (TEM) and the relative technical error of measurement (rTEM) were computed from the measures taken by the two experimenters for the 2nd and 4th digits in accordance with established protocol [25]. For 2D measurement TEM = 0.49 and rTEM = 0.65%, for 4D measurement TEM= 0.46 and rTEM = 0.61%, indicating an acceptable level of precision (below 5%) [25]. Mean values for the right hand and left hand digit ratios were 0.962 (SD= 0.027) and 0.970 (SD= 0.021) respectively, comparable with reported means for a male sample in the literature. No significant relationships were observed between left or right hand 2D:4D ratio and vocal measures.

4. Discussion

The current study provides supporting evidence of a significant negative relationship between daily mean values for fundamental frequency and circulating testosterone as well as individual measures at 9am and 3pm (with a trend towards significance at 12 noon); higher testosterone indicating lower fundamental frequency. Some indication of a negative relationship between the daily mean values for formant dispersion and circulating testosterone was also observed although this did not reach significance and no relationship was observed between the two measures at individual time points during the day. There was a significant effect of time of day on testosterone as expected and also a significant effect of day on fundamental frequency but not formant dispersion suggesting a novel finding for diurnal variation in fundamental frequency. Results also suggest a trend towards an association between the fall in testosterone throughout the day and the rise in fundamental frequency although this relationship did not reach significance. No relationship was observed between vocal parameters and early exposure to testosterone (as measured by 2D:4D ratio).

In support of previous findings [14,15] a significant negative relationship between various measures of circulating testosterone and fundamental frequency was found although the magnitude of the relationships in the current study were generally larger than those observed in previous research which report correlation coefficients of -0.35 [14] and -0.26 [15]. Such differences appear to be dependent upon the time of sampling with correlation coefficients in the current study of -0.51 in the early morning and -0.36 in the afternoon. Further, a diurnal variation in fundamental frequency that appears to reflect the diurnal variation in circulating testosterone was observed but, as would be predicted, in the opposite direction. An association approaching significance between the fall in testosterone levels throughout the day and the rise in fundamental frequency was also observed. Such diurnal variation in fundamental frequency might explain previous contradictory findings for a relationship between circulating testosterone and fundamental frequency in past research when time of day has not been controlled. It may also explain the difference in magnitude of the relationship between the findings of the current study and previous work. Certainly, these finding suggest that any future examination of the relationship between vocal frequencies and circulating levels of testosterone should consider time of day as a factor. In the current study, testosterone was measured three times across a single day, however, since levels of testosterone may vary over very short periods of time future research should consider the possibility of a greater number of testing times throughout the day to provide a daily profile of both measures with which to examine diurnal variation. In addition, the recruitment of a larger sample should also be a consideration.

Results of the current study found a trend approaching significance for a negative relationship between a daily mean value for testosterone and a daily mean value for formant dispersion, higher testosterone indicating smaller formant dispersion although no relationship between the two measures at individual time points providing some limited support for the findings of Bruckert and colleagues [16]. Findings of the current study suggest that the relationship between circulating testosterone and fundamental frequency is more apparent than that between circulating testosterone and formant dispersion. This may perhaps be a reflection of the relative importance of testosterone to the changes that take place in the male larynx during puberty with testosterone being more directly implicated in changes to the vocal folds that influence fundamental frequency than in the changes to the vocal tract that influence formant frequencies. Testosterone is thought to play a role in the descent of the larynx although other factors including growth hormone are also likely to be involved [9]. In addition generalised somatic growth of the resonance chambers is also under the influence of a number of factors [8].

Results of the current study confirm that circulating levels of testosterone continue to be related to vocal frequencies in adult males following puberty. Studies examining the direct effects of testosterone intervention on vocal changes in both males and females during adulthood also suggest plasticity, for example, treatment for male hypogonadism (testosterone deficiency) is known to permanently lower the fundamental frequency of male patients [26,27]. Following an injection of testosterone in females irreversible masculine vocal characteristics are produced [8] and under the influence of androgens following the hormonal shift at menopause, the voices of post-menopausal women may also deepen [26].

In agreement with previous findings [22] the current study found no relationship between 2D:4D (a biomarker of prenatal testosterone exposure) and any vocal parameter measured. Although a null finding does not necessarily mean that there is no relationship, the available evidence thus far suggests that the prenatal hormone environment may not influence the adult male voice. Since sexual dimorphism of the voice to a large extent only occurs following puberty this finding is not unexpected. In the current study 2D:4D ratio was measured by two experimenters from printed scans using digital callipers. There has been some discussion in the literature about the use of scans or photocopies for 2D:4D measurement. This protocol reduces sampling times, removes the necessity for two independent researchers to be present at testing sessions and provides a permanent facsimile of the hand. Comparisons of measurements of 2D:4D from photocopies and directly from fingers show high interclass correlation coefficients [28] although measures from photocopies are thought to produce lower 2D:4D values [29]. The recommendation is that the two methods should not be combined in one study or used together in comparative studies [29], which was not the case in the current study.

In conclusion, results of the current study support previous findings for a relationship between circulating levels of testosterone and adult male fundamental frequency. It also provides some limited evidence for a relationship between circulating testosterone and formant dispersion (although this did not reach statistical significance) but no evidence for a relationship between the prenatal hormone environment (as measured by 2D:4D ratio) and vocal frequencies. Novel findings of diurnal variation in fundamental frequency that appears to reflect the diurnal variation commonly observed in testosterone suggest that time of day should be an important consideration in future studies examining vocal frequencies. Finally, taken together, the findings of the current study support the proposition [3] that male vocal frequencies, in particular fundamental frequency, may provide an honest signal of the speaker's hormonal quality. It is thought that men's voices may have deepened over the course of evolution in order to signal dominance [30, 31] and/or to increase the speaker's attractiveness [3]; playing an important role in human interaction in the context of courtship and competition.

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